

DIV. OF HERPETOLOGY

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Age and Growth of the Brook Trout in a Wyoming Beaver Pond¹

GEORGE H. ALLEN

PARTLY because of its preference for cold-water habitats, the brook trout (*Salvelinus fontinalis*) has been widely introduced into spring creeks, beaver ponds, and high altitude lakes and streams in western North America. Beaver ponds have always been one of the favorite planting sites. The inaccessibility of these populations of brook trout, to fishermen and biologists alike, has placed their management on a conjectural basis in most instances. The literature on brook trout contains little information on populations in beaver ponds. Beaver-trout relationships have been the subject of debate, but with almost no supporting data. This paper, in presenting information on a relatively undisturbed brook trout population in a small Wyoming beaver pond, attempts to remedy some of these deficiencies.

DESCRIPTION OF POND

The pond lies at an elevation of 8,000 feet, on the eastern flank of the Medicine Bow Mountains, roughly 80 miles west of Cheyenne, Wyoming (Fig. 1). In the area a series of small beaver ponds impound the waters of Spring Creek, a small tributary of the South Fork of Little Laramie River. Waters from a number of springs issuing from the base of the hills immediately to the south of Spring Creek are also impounded. Information furnished by the Wyoming Game and Fish Department (personal communication) is that the summer flows in Spring Creek are approximately 5-6 cubic feet per second, with temperatures between 50° and 56° F. The springs are considerably colder, but no temperature data are available. The area of the beaver pond under consideration was not over one quarter of a surface acre. A maximum depth of six feet occurred immediately upstream from the face of the dam, while the average depth was approximately three feet. The pond bottom was of black organic debris in a layer up to several feet thick.

Clumps of willow (*Salix* sp.) surround the pond edges, with clumps of both live and dead willows interspersed throughout the inundated area. As these ponds are accessible only through private land and are close to other excellent fishing water in the Medicine Bow National Forest, they are subjected to negligible fishing pressure.

COLLECTION OF SAMPLE

On September 9, 1952, field crew members of the Wyoming Game and Fish Department dynamited the dam of the beaver pond. Sixty-two brook trout were collected from isolated pools of water formed after the rapid recession of the water level. The fish were packed in moss and placed in 10-15 per cent formalin 10 hours after collection. Several months later the fish were weighed and measured.

Rapid draining of the beaver pond provided the opportunity for fish in every age group to become stranded in the moss and algae of the pond bottom or trapped in isolated pockets and pools of water left by the receding water. No larger or smaller fish than those collected were present in the tributary stream above the dam or in the stream and spring flows running through the drained pond. The entire drained area of the beaver pond was visited six times during the day. As large numbers of fingerlings were observed in the stream above the beaver pond, it is presumed that the sample does not represent the true relative abundance of the younger age groups.

STRUCTURES USED IN AGE STUDIES

Age analyses were made by studying scales from two different body areas and by examining opercular bones. Small scrapings of scales were taken from analogous "key" locations on the left and right sides of each fish, at a point 4 to 5 scale rows above the lateral line in the vertical plane passing through the middle of the adipose fin (positions LA and RA for left and right sides, respectively). Up to five nonregenerated

¹ Contribution No. 9, School of Fisheries, University of Washington.

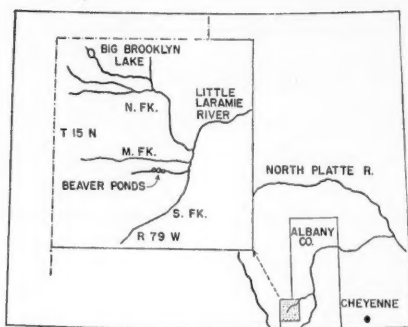


Fig. 1. Map showing location of beaver ponds, Albany County, Wyoming.

scales from each area were cleaned and mounted on a microscope slide in a drop of water. Slide and cover slip were held in place by strips of cellulose tape, and the mount was allowed to dry. The scales remained flat, provided that the drying process was slow. Mr. T. S. Koo of the Fisheries Research Institute, University of Washington, in studying the scales of downstream migrants of red salmon (*Oncorhynchus nerka*), has also found that direct mounting is the most acceptable method for studying small scales. For the LA position, the clearest scale from those mounted for each fish was projected at a magnification of 100 diameters directly onto Kodabromide F2 paper, and age readings were made from these prints.

The left opercular series, consisting of the opercle, subopercle and interopercle, was removed, cleaned and mounted directly between two slides. The entire element was then projected at a magnification of eight diameters directly onto F5 Kodabromide paper. Reduced aperture required exposure times up to 120 seconds depending upon thickness and coloration of the structure. Age readings were made from these prints.

Scales from the right side of the fish (position RA) were prepared similarly to LA-position scales as mentioned previously. Age readings, however, were made directly by projecting the scales to a magnification of 260 diameters.

All prints and mounted aging structures were identified only by number. The preservative in one jar of specimens became contaminated, resulting in darkly stained opercles which produced very poor prints (Pl. I, Fb); in such cases,

prints of right opercular elements were substituted.

REGENERATED SCALES

It is well known that regeneration occurs in a high percentage of brook trout scales. From 22 of the larger specimens, samples of LA scales and samples of scales from an LD position (halfway between the anterior insertion of the dorsal fin and the lateral line) were compared as to frequency of regenerated scales (Table I). Utilizing the total and sub-total numbers of non-regenerated and regenerated scales from the LA and LD positions, chi-square tests indicate that, for all fish combined, a higher percentage of non-regenerated scales was found for the LA position (caudal peduncle), and that female fish exhibited a higher percentage of non-regenerated scales for the LA position

TABLE I
NUMBERS OF NON-REGENERATED AND REGENERATED SCALES ON BROOK TROUT IN SAMPLES FROM LA AND LD POSITIONS

| Fork length in mm. | Sex | LA position | | LD position | |
|-----------------------|----------|-------------|------|-------------|------|
| | | Non-reg. | Reg. | Non-reg. | Reg. |
| 131 | F | 23 | 10 | 42 | 18 |
| 133 | M | 20 | 2 | 19 | 18 |
| 134 | M | 27 | 23 | 19 | 26 |
| 139 | F | 27 | 10 | 26 | 34 |
| 140 | F | 8 | 17 | 35 | 25 |
| 140 | F | 33 | 8 | 23 | 11 |
| 142 | M | 20 | 7 | 10 | 29 |
| 145 | M | 12 | 11 | 11 | 36 |
| 146 | M | 19 | 8 | 9 | 23 |
| 146 | M | 25 | 16 | 25 | 21 |
| 150 | F | 16 | 20 | 16 | 48 |
| 150 | F | 20 | 4 | 12 | 65 |
| 154 | M | 7 | 10 | 10 | 21 |
| 160 | F | 26 | 39 | 46 | 29 |
| 161 | M | 13 | 22 | 5 | 15 |
| 168 | F | 26 | 6 | 1 | 66 |
| 169 | F | 36 | 3 | 24 | 28 |
| 170 | M | 3 | 37 | 3 | 45 |
| 170 | F | 12 | 19 | 4 | 40 |
| 174 | M | 13 | 25 | 3 | 21 |
| 174 | F | 26 | 10 | 21 | 64 |
| 207 | F | 3 | 13 | 0 | 66 |
| Totals | F (12) | 256 | 159 | 250 | 494 |
| | M (10) | 159 | 161 | 114 | 255 |
| | M+F (22) | 415 | 320 | 364 | 749 |

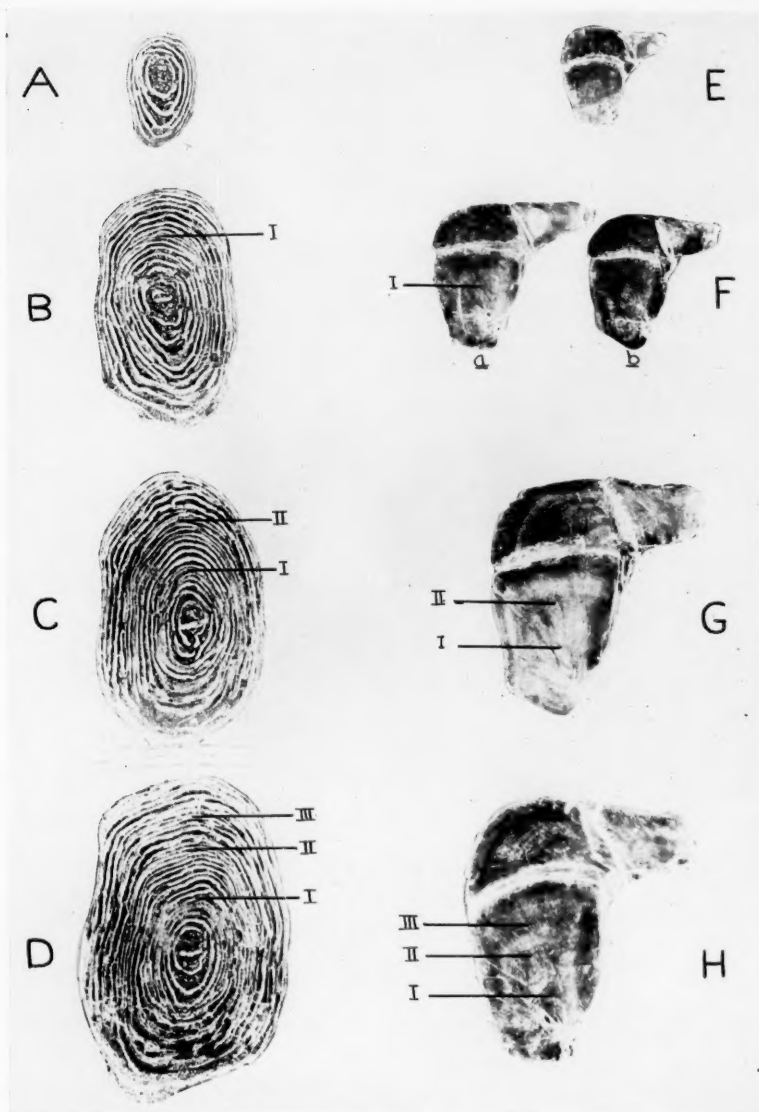


PLATE I

Right adipose (RA) scales and opercles of brook trout taken from a Wyoming beaver pond.

A, E—male, 76 mm. fl. len., age-group 0; B, Fb—male, 94 mm. fl. len., age-group I; Fa—female, 98 mm. fl. len., age-group I; C, G—male, 161 mm. fl. len., age-group II; D—male, 182 mm. fl. len., age-group III; H—female, 195 mm. fl. len. age-group III.

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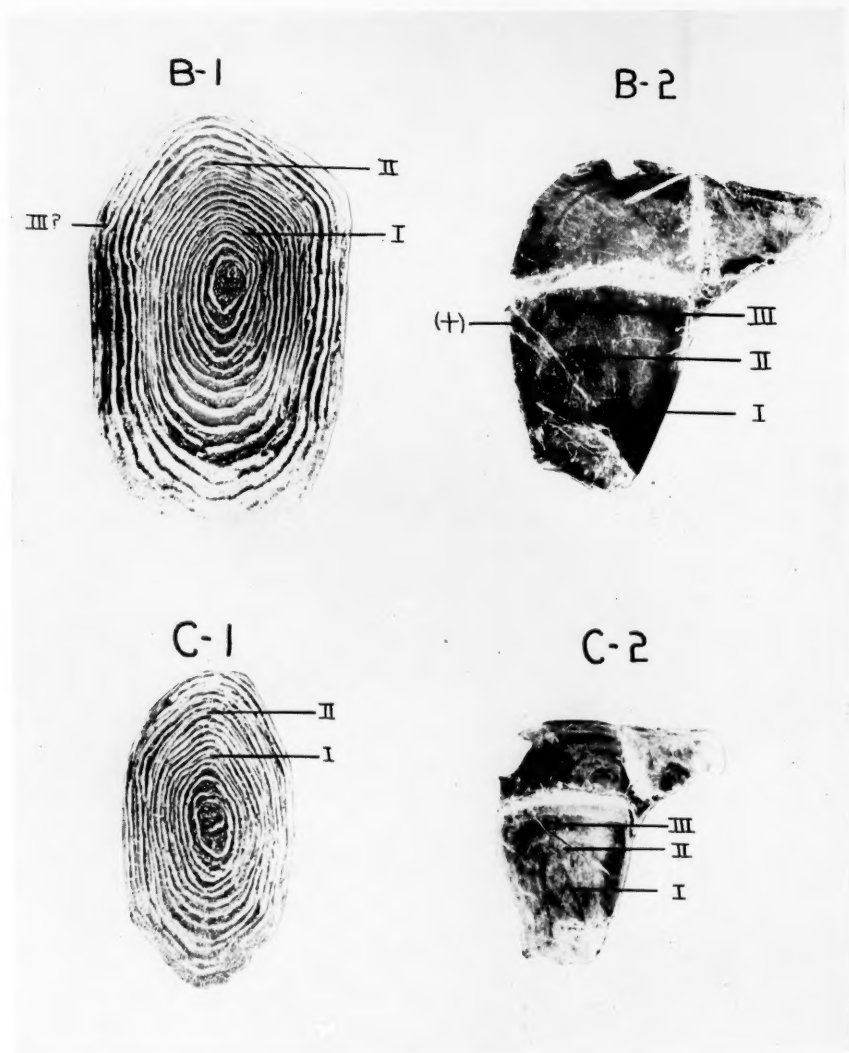


PLATE II

Comparison of right adipose (RA) scales and opercles from brook trout representing points B and C of Figures 3 and 4.

B-1, B-2—Point B, female, 207 mm. fl. len.; C-1, C-2—Point C, female, 150 mm. fl. len.

than did males. Cooper (1951) and Elson (1939) recommended collecting scales of the brook trout for growth studies from above and below the lateral line in the region of the caudal peduncle, on the basis that the first appearance of scales takes place in this region.

DEFINITION OF ANNULUS

In discussing the definition of the annulus as applied to brook trout scales, Cooper (1951: 143) stated, "the crowding of adjacent circuli, irregularity or incompleteness in their formation, and the 'cutting over' of circuli in the postero-lateral areas, are the chief characteristics that have been employed." He further wrote that, "The criterion most useful to me was the sudden change in growth pattern of the circuli." In the present study, no single characteristic mentioned above could consistently be applied in identifying the annulus. A combination of all characteristics had to be utilized. The growth rate differed sufficiently between winter and summer to produce zones within which the circuli are thin and crowded and zones within which the circuli are widely spaced. Associated with the zones of thin and closely crowded circuli there are irregular and incompletely formed circuli, and circuli which "cut over" in the antero-lateral areas. Consequently the aging procedure using scales involved a degree of subjectivity in recognition of the annulus. Thin, crowded circuli, between two zones of more-widely spaced circuli, usually associated with incomplete circuli and circuli which "cut over" in the antero-lateral areas, defined the annulus of the scales.

The opercular elements were photographed to bring out broad light and dark areas on the print. The lighter zones of the print were thought to represent summer growth and the dark zones winter growth. Thus, the dark bands were considered to be the annuli. This definition of the annulus is predicated upon the untested assumption that rapid growth produces bone which transmits light less readily than does bone formed during periods of slow growth. As the kodabromide print is essentially a negative, the dark areas of the opercular elements of Plates I and II would correspond to light areas on a normal photographic print of these opercular elements, and vice versa. Only a few of the opercular elements showed any dark or

light bands when examined either with or without a microscope.

Basis for assigning fish to an age group was the number of completely formed annuli. Calendar age is approximately 9 months more than indicated by the age group.

DEPENDABILITY OF AGE READINGS

Independent age readings were compared, and disagreements between readings were resolved in a joint reading in which all three structures (opercle, LA scales and RA scales) were reexamined. The following is the summary of agreements and disagreements of the independent (i.e., first) readings of the three structures:

| | |
|---------------------------------|----|
| I. Complete agreement..... | 42 |
| II. Disagreement..... | |
| a. Agreement in 2 out of 3..... | 16 |
| b. No agreement..... | 4 |
| Total..... | 62 |

For the 20 fish under II above, a joint reading of the three structures reaffirmed the original age determinations on 12 of the 16. These 12 readings plus the 42 complete-agreement readings give 54 readings which are regarded as dependable. Of the remaining eight fish, a decision on age was reached for five, while three had to be read jointly a second time to reach a decision. Disagreements tended to increase with the older age groups.

VALIDITY OF ANNULI

The validity of the annuli or "marks" as being true "year marks," that is marks formed only once a year, cannot be stated categorically. Inferences can be made, however, indicating that the annuli as defined are actually "year marks."

In applying the criterion developed by Petersen (1895), the length-frequency distributions for each age, when compared with the modes in the length-frequency distribution for the sample, exhibit reasonable correspondence (Fig. 2). Assumptions necessary for a valid use of the Petersen Method are met in part. The sampling was over a short period of time. Spawning is once annually and over a limited time. Uniform growth within and between year classes has to be assumed, although this assumption appears valid. The modes of the length-frequency distribution for the popula-

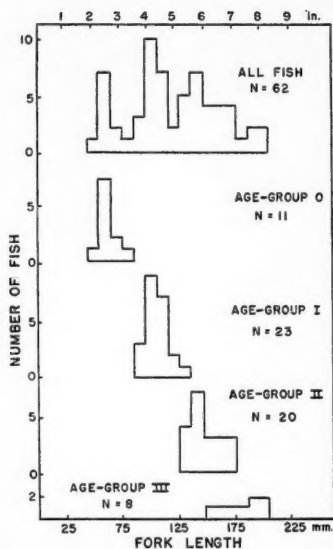


Fig. 2. Total-length frequency of sample and length frequency by age of brook trout from a Wyoming beaver pond.

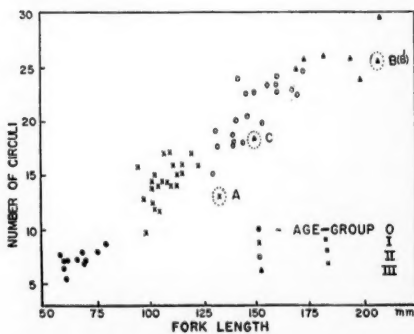


Fig. 3. Relationship between average number of circuli in the anterior scale radius of right adipose (RA) position scales and length of fish by age group of brook trout from a Wyoming beaver pond. (For discussion of fish A, B, B' and C, see text.)

tion are distinct (Fig. 2), while the average number of circuli in the anterior field of the RA scales plotted against fork length indicate uniform growth within and between year classes (Fig. 3). Counts of circuli in the anterior scale radius, for all RA scales which were mounted, were averaged. Although this analysis is indicative of uniform growth between and within year classes, it is not conclusive proof, as this

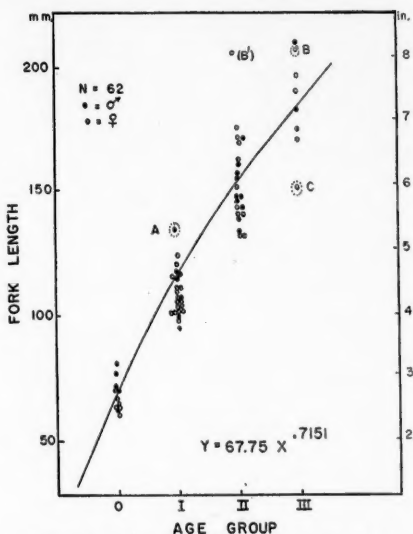


Fig. 4. Rate of growth, sexes combined, of brook trout from a Wyoming beaver pond. (For discussion of fish A, B, B' and C, see text.)

would infer that the agings were all known to be correct.

DIFFICULTIES IN AGING PROCEDURE

On initially constructing Figure 4, several points appeared markedly aberrant, especially those designated A, B' and C. The letters B and C of Figures 3 and 4 represent the same two fish, the scale and opercle from which are reproduced on Plate II. B' represents the aging of fish B by the procedure previously described, and the position on the growth curve as originally constructed. In order to check the validity of the age readings producing these points (A, B' and C), Figure 3 was constructed to show the relationship between mean number of circuli in the anterior scale radius of RA scales, fork length, and age. Apparently the error in aging fish B occurred in the scale readings, which were consistently read as age-group II. The annulus designated 3? was considered incompletely formed (Pl. II, B-1). Examination of Plate II, B-2, however, indicates the opercle having 3 annuli, in addition to a small amount of summer growth along the lateral edge of the opercle (Pl. II, B-2 +). Reexamination of the scales of 5 fish in age-group III showed the spacing of the circuli and position of the annuli

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to resemble that of scale D, Plate I. Due to a large third-summer growth followed by a slight fourth-summer growth, it appears that fish B was aged incorrectly by the methods employed because of the annulus near the edge of the scale being interpreted as incomplete. Consequently fish B was reassigned to age-group III.

In the case of point C in Figures 3 and 4, aging was difficult using scales but consistently gave age-group III with opercles. Two annuli are readily distinguished on RA scale (Pl. II, C-1); however, the crowded circuli made it difficult to designate an annulus beyond that marked II. "Cut over" circuli near the edge of the scale in the antero-lateral areas were also interpreted as an annulus just forming. Again the opercle showed three distinct annuli. On this basis no change in the aging of fish C was made.

For point A, the ages from the three independent readings were in agreement.

TIME OF ANNULUS FORMATION

Annuli in the process of formation were evident on the edges of both scales and opercles. Circuli were becoming more closely spaced, with incomplete and "cut over" circuli appearing on the edges of the scales. Dark zones were showing along the edges of the opercles. Cooper (*loc. cit.*) stated that annulus formation in the brook trout populations studied in Michigan takes place in April, May and June, with the appearance of the scale changing little from September until spring. It would appear that the brook trout in the present study produce similar patterns of scale growth.

False annuli were not considered present on the scales of the brook trout under consideration.

AGE AND LENGTH AT FIRST ANNULUS

Robertson (1947), Curtis (1935), and Brown and Bailey (1952) have reported trout populations in which fish did not develop scales by the end of the first year of life. The assumption has been made in this study that the first mode in Figure 2 represents young of the year. A false assumption would mean that a group of fish, neither sampled nor observed, of average length less than 45 mm. existed in the pond. It would also require that growth in the second

year would be roughly only 20 mm. These possibilities seem unlikely. The smallest mode (Fig. 2) falls within the average size of first-year survivors of naturally spawned brook trout collected in Convict Creek, California, during September in the years 1940 to 1946 (Smith, 1947). Convict Creek lies at an elevation of 7,200 feet and the Wyoming beaver pond at 8,000 feet. Furthermore, all aging structures from fish making up the first mode showed no annulus.

On September 9, 1952, the author collected nine brook trout of age group 0 from a small tributary stream flowing into the west end of Big Brooklyn Lake (Fig. 1). These fish, averaging 46 mm. in fork length with a range of 36 to 51 mm., had scales along the lateral line that averaged 0.065 by 0.35 mm. in shortest and longest diameter, and possessed two circuli. As Big Brooklyn Lake lies at an altitude of 10,500 feet, there should be sufficient difference in the growing season to account for the slower growth rate and scale development. These data, however, point out that it is possible to collect 0-age-group brook trout in September having an average length of less than 45 millimeters.

RATE OF GROWTH

The sexes were combined in calculating the rate of growth of the population, as there appeared to be no noticeable difference in growth rates between male and female fish (Table IV). The growth rate was expressed as a curve of the form $Y = aX^b$, where Y is the mean length in millimeters of the fish at each age, X is the age of the fish, and a and b are constants determined empirically. The equation in logarithmic form is:

$$\text{Log } Y = +0.71508 \text{ Log } X + 1.83092$$

The growth curve and equation are given in the non-logarithmic form in Figure 4.

LENGTH-WEIGHT RELATIONSHIP

Weights of the smallest 11 fish were taken to the nearest tenth of a gram in order to eliminate the possibility of large percentage errors, while the others were weighed to the nearest gram. Utilizing an equation of the form $Y = aX^b$, where Y is the weight in grams, X is the fork length in millimeters, and a and

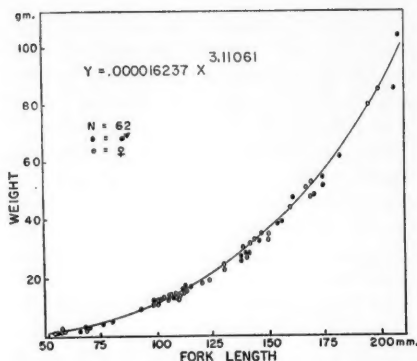


Fig. 5. Length-weight relationship of formalin-preserved brook trout from a Wyoming beaver pond.

b are constants determined empirically, the equation in its logarithmic form is:

$$\log Y = -5.21050 + 3.11061 \log X$$

This relationship between length and weight as fitted from the actual data (Table V) is shown graphically (Fig. 5). No corrections for the effects of preservation on weights and lengths were made.

FECUNDITY

Fecundity was determined by removing ovaries and counting all eggs. As the brook trout spawns during the fall of the year, presumably the ovaries were well developed in those fish which would have spawned during the fall of 1952. The ovaries in mature females filled the body cavity back to the vent, as did the testes in mature males.

Little appears in the literature on the fecundity of brook trout. Smith (*loc. cit.*), in studying returns from natural spawning of brook trout, encountered difficulty in obtaining estimates of expected numbers of eggs deposited by his fish. He stated, "Unfortunately, the best estimate is none too good, because very little has been done on the correlation between numbers of eggs and sizes of eastern brook trout." Counts of eggs from 29 female fish from 5 to 15 inches in length, representing populations in North Carolina, California and Ontario, were utilized by Smith to obtain a curvilinear relationship between size of female and number of eggs produced.

Two equations were fitted to the fecundity

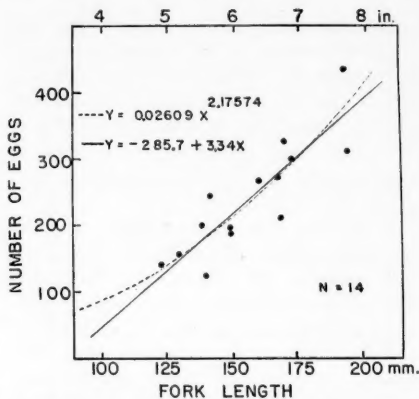


Fig. 6. Fecundity of brook trout from a Wyoming beaver pond.

data for the brook trout from the Wyoming beaver pond:

| Relationship | Equation | Standard error of estimate |
|--------------|--------------------------|----------------------------|
| Rectilinear | $Y = -285.7 + 3.34X$ | 42.74 |
| Curvilinear | $Y = 0.02609X^{2.17574}$ | 42.15 |

Y is the number of eggs; X is the fork length in millimeters.

It may be seen that the number of eggs and length of female are adequately expressed as a rectilinear relation (Fig. 6). This result is at variance with data presented by Ricker (1932), Vladikov and Legendre (1940), and Smith (1947), all of whom expressed fecundity in the brook trout as curvilinear. Ricker, in constructing his Figure 4, utilized, in part, data from Titcomb (1897) to apparently fit by hand a curvilinear relationship. Titcomb's data², however, actually indicate a rectilinear relation, with following calculations being made from his data:

| Equation | Standard error of estimate |
|----------------------|----------------------------|
| $Y = -2,679 + 11.7X$ | 224.95 |

Y is the number of eggs; X is length in millimeters (total length presumably).

Titcomb's data, however, have been of limited value because the author stated that "some of these trout had apparently dropped part of their eggs before being captured." The relative dispersion (coefficient of variation) in

² Data from pages 83-84. One egg count, appearing aberrant, was not included in the calculations.

TABLE II
FECUNDITY OF BROOK TROUT FROM A WYOMING
BEAVER POND

| Fork length in mm. | Number of eggs | | |
|--------------------|----------------|-------------|-------|
| | Left ovary | Right ovary | Total |
| 124 | 55 | 87 | 142 |
| 130 | 74 | 81 | 155 |
| 139 | 91 | 109 | 200 |
| 140 | 64 | 60 | 124 |
| 143 | 120 | 127 | 247 |
| 150 | 87 | 107 | 194 |
| 150 | 96 | 92 | 188 |
| 160 | 122 | 145 | 267 |
| 168 | 121 | 148 | 269 |
| 169 | 117 | 97 | 214 |
| 170 | 156 | 170 | 326 |
| 174 | 144 | 155 | 299 |
| 195 | 154 | 158 | 312 |
| 198 | 245 | 196 | 441 |

the rectilinear relationships expressing fecundity of brook trout from a Wyoming beaver pond and a 1,500-acre lake in Vermont are as follows:

| Locality | C. V. |
|---|-------|
| Wyoming beaver pond trout | 27% |
| Vermont Lake (Titcomb, <i>loc. cit.</i>) | 66% |

Data from Vladikov and Legendre (*loc. cit.*), fitted to a curvilinear relation, produced much lower estimated numbers of eggs for a given length than did the present study or the relationship developed by Smith (*loc. cit.*).

The number of eggs counted in left and right ovaries exhibited considerable variation, with ten fish having higher counts for the right ovary and four having lower counts (Table II).

AGE AT MATURITY

Sex of immature fish was established by microscopic examination of the gonads. Small, immature eggs could be ascertained in gonads of females, contrasted to a homogenous mass of tissue in male gonads. Maturity at each age is presented in Table III.

SIGNIFICANCE TO BEAVER-TROUT MANAGEMENT

Ricker (1932: 73) stated, "The maximum size to which a speckled trout (*Salvelinus fontinalis*) attains is apparently to be correlated with the size of the body of water in which it lives, and

TABLE III
AGE, SEX AND STAGE OF MATURITY OF 62 BROOK
TROUT FROM A WYOMING BEAVER POND

| Age group | Female | | Male | |
|-----------|--------|------|------|------|
| | Imm. | Mat. | Imm. | Mat. |
| 0 | 5 | .. | 6 | .. |
| I | 15 | 1 | 3 | 4 |
| II | 2 | 9 | .. | 9 |
| III | .. | 5 | .. | 3 |

TABLE IV
RATE OF GROWTH IN BROOK TROUT FROM A
WYOMING BEAVER POND
Fork lengths in millimeters

| Age group | Male | | | Female | | |
|-----------|----------------|---------|----------------|----------------|---------|----------------|
| | Average length | Range | Number of fish | Average length | Range | Number of fish |
| 0 | 70 | 60-80 | 6 | 63 | 59-69 | 5 |
| I | 111 | 94-134 | 7 | 108 | 98-124 | 16 |
| II | 150 | 133-170 | 9 | 150 | 130-174 | 11 |
| III | 188 | 174-209 | 3 | 184 | 150-207 | 5 |

more closely perhaps, with the presence of suitable large food: i.e., fish or crayfish." Kendall and Dence (1927: 442) wrote, "Furthermore it has been learned that as a rule trout of small streams and the restricted upper waters of larger streams do not grow so fast as those in less circumscribed waters," but they also mentioned that differences in growth may be due to feeding conditions. If the size of the lake or stream in which brook trout occur actually influences the capacity of the species to attain a large size (i.e., over seven inches), a revision in stocking policies for many waters now considered best suited to brook trout would be in order. Other studies in which the brook trout living in small ponds and streams seldom attained "desirable" lengths and died at very young ages as compared to other species of trout include Hoover (1939), Shetter and Leonard (1943), Hazzard (1933), Shetter and Hazzard (1939), Kendall and Dence (1927), and Moore et al. (1935). It is suggested that in stocking small ponds and streams which are subjected to only slight fishing pressures, emphasis might be placed on species of trout which have been found to grow to larger average lengths than the brook trout under similar con-

TABLE V
LENGTH, WEIGHT, SEX, AGE AND MATURITY OF
BROOK TROUT FROM A WYOMING BEAVER POND

| Age Group | Sex | Fork length in mm. | Weight in gms. | Mat. |
|-----------|-----|--------------------|----------------|-----------|
| 0 | M | 60 | 2.0 | Imm. |
| | | 67 | 2.5 | Imm. |
| | | 69 | 3.0 | Imm. |
| | | 70 | 2.7 | Imm. |
| | | 76 | 4.0 | Imm. |
| | | 80 | 4.7 | Imm. |
| | F | 59 | 2.0 | Imm. |
| | | 61 | 2.0 | Imm. |
| | | 62 | 2.1 | Imm. |
| | | 63 | 2.5 | Imm. |
| | | 69 | 2.8 | Imm. |
| I | M | 94 | 10.0 | Imm. |
| | | 107 | 14.0 | Imm. |
| | | 116 | 17.0 | Imm. |
| | | 99 | 12.0 | Mat. |
| | | 113 | 16.0 | Mat. |
| | | 114 | 18.0 | Mat. |
| | | 134 | 27.0 | Mat. |
| | F | 98 | 11.0 | Imm. |
| | | 102 | 12.0 | Imm. |
| | | 102 | 12.0 | Imm. |
| | | 102 | 11.0 | Imm. |
| | | 103 | 13.0 | Imm. |
| | | 104 | 13.0 | Imm. |
| | | 105 | 12.0 | Imm. |
| | | 105 | 13.0 | Imm. |
| | | 107 | 14.0 | Imm. |
| | | 109 | 14.0 | Imm. |
| | | 110 | 14.0 | Imm. |
| | | 110 | 12.0 | Imm. |
| | | 112 | 15.0 | Imm. |
| | | 114 | 16.0 | Imm. |
| | | 120 | 13.0 | Imm. |
| | | 124 | 19.0 | Mat. |
| II | M | 133 | 26.0 | Mat. |
| | | 142 | 28.0 | Mat. |
| | | 145 | 33.0 | Mat. |
| | | 146 | 32.0 | Mat. |
| | | 146 | 34.0 | Mat. |
| | | 154 | 38.0 | Mat. |
| | | 155 | 39.0 | Mat. |
| | | 161 | 48.0 | Mat. |
| | | 170 | 49.0 | Mat. |
| | F | 131 | 23.0 | Imm. |
| | | 149 | 27.0 | Imm. |
| | | 139 | 24.0 | Mat. |
| | | 139 | 30.0 | Mat. |
| | | 140 | 28.0 | Mat. |
| | | 143 | 32.0 | Mat. |
| | | 150 | 33.0 | Mat. |
| | | 160 | 45.0 | Mat. |
| | | 168 | 51.0 | Mat. |
| | | 170 | 53.0 | Mat. |
| | | 174 | 55.0 | Mat. |
| III | M | 174 | 52.0 | Mat. |
| | | 182 | 62.0 | Mat. |
| | | 209 | 105.0 | Mat. |
| | F | 150 | 35.0 | Mat (C)* |
| | | 169 | 49.0 | Mat. |
| | | 195 | 81.0 | Mat. |
| | | 198 | 86.0 | Mat. |
| | | 207 | 84.0 | Mat. (B)* |

* See section on difficulties in aging procedure.

ditions. In this respect, personal observation on a number of small ponds and streams in mountain areas of Wyoming have indicated that the cutthroat trout (*Salmo clarki*) reaches noticeably larger sizes than the brook trout in the same waters. These observations apply only to small streams and ponds in which the populations of brook trout have reached stability.

An adequate knowledge of how best to stock and manage beaver ponds should be a pressing topic for research by fish and game departments charged with the responsibility of such fisheries. Beaver-trout ecology has not received concentrated attention in the rocky mountain region, although the problems are frequently mentioned in non-technical literature. The relation of beaver to trout in eastern United States, as reported and discussed by Salyer (1935a, b), Johnson (1927), Bump (1941) and Cook (1940), cannot be generalized to include beaver-trout relations in the mountain states of the West. It is hoped that this fertile area of investigation will not long remain unattended and that studies additional to those underway at Sagenhen Creek, California (Anonymous, 1954) will be undertaken.

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The Hawaiian Fishes of the Family Moringuidae: Another Eel Problem¹

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INTRODUCTION

A SIMPLE attempt to identify the Hawaiian species of the family Moringuidae has brought us face to face with another "eel problem." In some ways our difficulties parallel those encountered many years ago with the freshwater eel (*Anguilla*), but in others they appear to be more complex. The biological problems in the Moringuidae have not passed unnoticed (cf. Parr, 1930: 14), nor are we able to give final answers to them. However, the improbability that such answers will be forthcoming in the near future leads us to present our data and preliminary interpretations here. These should at least serve as warnings concerning the pitfalls that lie in the road to moringuid classification.

Our data consist of two rather separate

segments. Those dealing with the Hawaiian material are primarily the responsibility of the senior author. The information on the large moringuid collections in the U. S. National Museum has been gathered by the junior author. These collections have been made available to us through the kindness of Dr. L. P. Schultz, to whom we are deeply obligated.

We should also like to thank the staff of the Pacific Oceanic Fishery Investigations for permission to use their X-ray apparatus, and Dr. George Henry of Honolulu for the donation of the X-ray film.

Up to the present time three different morphological types of moringuid eels have been taken in Hawaii. All three are known to us only from small patches of sandy bottom, to the surface of which they have been brought by the use of rotenone.

¹ Contribution No. 71, Hawaii Marine Laboratory.

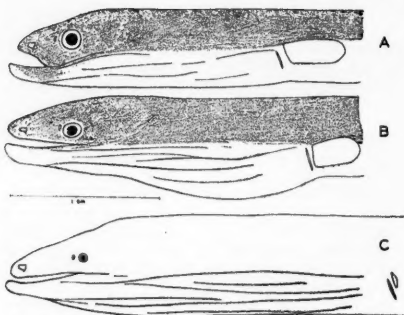


Fig. 1. Heads of three forms of Hawaiian *Moringua*. A—maturing male; B—maturing female; C—immature.

IMMATURE FORM

By far the commonest of the three different morphological forms is a yellowish, worm-like creature, with small embedded eyes and rudimentary fins (Figs. 1c and 2c). This type has been described as *Moringua hawaiiensis* by Snyder (1904: 517, pl. 3, fig. 6). More than a hundred specimens, ranging in length from 102 to 415 mm., have been taken by us in Hawaii at various seasons of the year (Table I). In its typical condition this form shows no indication of sexual maturity; though we have made repeated attempts to find gonads, we have either been totally unsuccessful or we have come to a rather dubious decision that the specimen was an immature female.²

One of the peculiarities found in the genus *Moringua* is that it may have the heart far behind the normal position below the pectoral fin bases. Apparently this is the only genus of eels, or of fishes for that matter, in which the heart shows a significant backward displacement. We have compared the gross structure of the heart of the above form (which has the heart well back as just described) with that of *Conger cinereus*. Aside from the weaker development of the pericardial membranes and the walls of the bulbus and ventricle of *Moringua*, no significant differences could be found. In both genera the heart seems to have essentially the same gross structure as that shown by Goodrich (1909: fig. 69F) for *Salmo*; there are no valves within the bulbus arteriosus itself.

² The fat bodies may be easily mistaken for female sex organs in these immature fishes, and certain identification of their gonads must await a more detailed histological examination than we have been able to make.

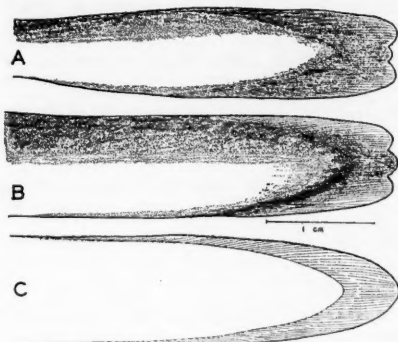


Fig. 2. Tails of three forms of Hawaiian *Moringua*. A—maturing male; B—maturing female; C—immature.

In the form of *Moringua* under consideration, the heart holds its usual position in relation to the liver (which lies directly behind the heart). Consequently the front of the liver also lies farther back than usual in the body. Directly behind the liver and gall bladder lies the elongate, I-shaped stomach with the pylorus far forward. The form and relative positions of the various digestive organs are similar to those found in other eels (cf. Suyehiro, 1942: 84-89), except that in *Moringua* most of the structures are more elongate.

MATURING FEMALES

The second of the three Hawaiian forms of *Moringuidae* is best represented by an apparently ripe female, 265 mm. long, taken off Waikiki on December 31, 1952. (This specimen was captured along with 20 immatures of the type previously discussed. These immatures ranged from 106 to 387 mm., and five of them were larger than the mature female; none of them could be sexed.) The ripe female (Figs. 1b and 2b) differs from the immature specimens in having the flesh over the eye clear rather than opaque, the eye itself larger (Table II), the pectoral fins well developed, a distinct but low dorsal and anal fin developed ahead of the caudal, and a trilobate tail. In coloration the specimen is dark above and silvery below. Internally, the heart is well back in the body, as in the immatures. Eggs fill much of the body cavity forward to the liver, and the stomach is present as a flabby, empty caecum.

Fortunately, a collection of *Moringua* taken

some ten miles from Waikiki on September 26, 1953, includes various intermediate stages between the immature and mature forms discussed above. It is apparent from this collection that the various features differentiating the ripe female from the immature, i.e., changes in coloration and in eye, fin, and egg size, all occur more or less concomitantly (Table II). In this collection once again some of the largest specimens show no sign whatever of maturing.

It seems to us that the specific identity of the two forms discussed above is certain. If this is correct, two features regarding them may be advantageously discussed here.

Taxonomically, the moringuid eels have often been divided into two sections, as by Weber and de Beaufort (1916: 337), depending upon whether the fins are rudimentary (*Aphthalmichthys*) or developed (*Moringua*). Whatever the situation may be with other species, the Hawaiian form apparently passes through both an *Aphthalmichthys* (immature) and a *Moringua* (mature) stage. Schultz (1953: 86, 88) did not divide the family into two sections, but did use the same characters of fin development to distinguish Marshallese species. Thus our immature Hawaiian form seems to be the same as Schultz's *Moringua abbreviata*, the mature female the same as *M. bicolor*, whereas Schultz's *M. macrocephala* represents an intermediate stage of maturity between the first two. (The Marshallese specimens identified as these three species have been reexamined by one of us).

Biologically, all of the changes that take place in the maturing female point to a change from a subterranean toward a pelagic existence. Further evidence for this supposition comes from the fact that mature (but so far as we know, no immature) moringuids have been taken at a night light in other regions (cf. Gordon, 1954: 12).

One other matter may be noted here. Our own data (Table I) indicate a seasonal spawning of the Hawaiian form of *Moringua*. If so, length frequency modes might well be expected among Hawaiian immatures. However, such modes are not obvious in the rather small samples of immatures available to us.

MATURING MALES

The third Hawaiian form is either the male of the forms just described, or it belongs to an

TABLE I
DATES OF CAPTURE (BY MONTH) OF THE THREE
HAWAIIAN FORMS OF MORINGUIDAE

| Form | Month | | | | | | | | | | | |
|------------------------|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | Jul. | Au. | Se. | Oc. | No. | De. | Ja. | Fe. | Ma. | Ap. | Ma. | Ju. |
| Immatures | .. | .. | X | .. | X | .. | X | X | .. | .. | X | X |
| Maturing females | .. | .. | X | .. | .. | X | .. | .. | .. | .. | .. | .. |
| Maturing males | .. | .. | .. | .. | .. | X | .. | X | .. | .. | .. | .. |

entirely different genus and species. It is represented by eight specimens 155 to 183 mm. in length. The first of these was taken on February 9, 1952, along with three representatives of the immature form previously discussed. Six more were collected from a rotenone station on December 31, 1952, together with 20 immatures and one ripe female. An eighth was taken on December 11, 1953, with 10 immatures.

There is a marked superficial resemblance between our mature males (Figs. 1a and 2a) and the mature females described above, in coloration, appearance of the eye, fin development, etc. Indeed Schultz (1953: 86, 88), while dividing up his species on the basis of sexual maturity, has included both males and females in at least two of them (*Moringua bicolor* and *M. macrochir*). Nevertheless the structural differences between our mature Hawaiian males and mature females are formidable. In the first place, the males are always much smaller than the females. In the adult males (but not the females) the upper lip projects down over the lower lip laterally. The maxillary teeth are lacking and the other dentition is reduced. Both the eye (Table II) and the head are relatively larger. There are about 6 fewer vertebrae and 7 fewer lateral-line pores on the average than in maturing females (Table IV). Finally, and probably most significantly, the heart in males is in its normal forward position. In almost all these features our males resemble the eel from the West Indies described as *Anguillichthys bahamensis* by Mowbray (in Breder, 1927: 10) and discussed at length by Parr (1930: 14), Trewavas (1932: 642), and most recently by Gordon (1954).³

³ Though the taxonomic status of the West Indian forms has been treated repeatedly, cf. Gordon (1954: 12), certain problems remain unanswered. As these are of some importance in connection with the present paper as well as for their own sake, they will be treated in some detail in the following paragraph.

The genus and species *Anguillichthys bahamensis* was described as new by Mowbray, who erected for it a new family,

TABLE II
CERTAIN FEATURES OF THREE HAWAIIAN FORMS OF MORINGUIDAE

| Sex and maturity | Locality and date | Standard length (mm.) | Pigmentation symbol | Eye diameter† | | Pectoral fin (in thousandths of S. L.) | | Caudal fin | Diameter of larger eggs (mm.) |
|------------------|-------------------------|-----------------------|---------------------|---------------|----|--|---------------|-------------|-------------------------------|
| | | | | A | B | Length | Width of base | | |
| Immature (♀?) | Waianae, Sept. 20, 1953 | 341 | 0 | 2.0 | 30 | 1.5 | 2.4 | Rounded | (None found) |
| " " | " " | 343 | 0 | 1.7 | 26 | 1.5 | 2.4 | " | " " |
| Maturing ♀ | " " | 327 | 1 | 3.1 | 45 | 3.4 | 3.4 | " | 0.2 |
| " " | " " | 336 | 1 | 3.3 | 44 | 5.1 | 3.6 | " | 0.2 |
| " " | " " | 346 | 2 | 2.9 | 43 | 2.9 | 3.2 | " | 0.2 |
| " " | " " | 368 | 2 | 3.3 | 50 | 6.0 | 4.4 | Subtruncate | 0.4 |
| " " | Waikiki, Dec. 31, 1953 | 265 | 3 | 4.9 | 65 | 9.4 | 4.5 | Trilobed | 0.5 |
| Maturing ♂ | " " | 159 | 2 | 6.3 | 59 | 20.7 | 8.2 | Bilobed | ... |
| " " | " " | 155 | 3 | 10.3 | 84 | 25.8 | 12.2 | " | ... |
| " " | " " | 156 | 3 | 10.2 | 84 | 25.0 | 12.2 | " | ... |
| " " | " " | 174 | 3 | 10.3 | 86 | 25.2 | 8.6 | " | ... |
| " " | " " | 177 | 3 | 7.9 | 70 | 20.8 | 8.5 | " | ... |

* 0 represents plain yellowish pigmentation; 3, blackish above and silver below; and 1 and 2, intermediate color phases.

† A = thousandths of standard length; B = thousandths of head length.

However, when the U. S. National Museum material (mostly from the Marshalls) of what appears to be the same species as found in Hawaii is investigated, it is discovered that

Anguillichthyidae. There seems to be nothing in Mowbray's description to distinguish this family from the Moringuidae. Parr (1930: 14) recorded further specimens of Mowbray's species, some of which were taken at a night light together with a ripe female eel (similar to our ripe female form). Parr identified the Bahamas female as *Stilbiscus edwardsi* Jordan and Bollman (1889: 549), the holotype of which is a maturing female with well-developed eggs. Parr sexed several of his *Anguillichthys*-type eels and found them all to be running-ripe males. On the basis of the similarities between *Anguillichthys bahamensis* and *Stilbiscus edwardsi*, and because both have been taken at the same night-light station, Parr synonymized *Anguillichthys* with *Stilbiscus*, strongly suggesting that the two forms may actually represent males and females of the same species (though he provisionally maintained them as distinct but congeneric). After dissecting "*Anguillichthys*," but not "*Stilbiscus*," Parr proposed the family name *Stilbiscidae* for the two forms. His definition of the family is as follows: "Closely related to the Moringuidae from which the present family mainly differs in having the parasphenoids well separated from the frontals, and in the peculiar differentiation of the vertical fins." As Trewavas (1932: 646) has noted, the nature of the vertical fins does not distinguish the *Stilbiscidae* from the Moringuidae. The osteological character given by Parr needs fuller consideration. In at least some other eels this particular character has no value; for example, various specimens of a single species of *Anguilla* may show either the moringuid or the stilbiscid form of the frontal-parasphenoid feature given by Parr (cf. Regan, 1912: 378). Nevertheless, this does not prove the character valueless in the eel group under discussion. Indeed, Trewavas' work indicates that it may well serve to distinguish Mowbray's *Anguillichthys* from *Moringua*. But what is the status of this character in *Stilbiscus edwardsi*? Does *Stilbiscus* have the character on which Parr erected the family *Stilbiscidae*? Is the character simply related to the sex of the individual? Trewavas (*loc. cit.*) has solved the difficulties arising from these questions at the family level by synonymizing both the *Stilbiscidae* and the *Anguillichthyidae* with the Moringuidae. The question remains of whether the genera *Anguillichthys* and *Stilbiscus* are separate and valid, whether one should be synonymized with the other, or whether one or both should be synonymized with *Moringua*.

many of the differences between males and females partially break down (compare Tables II and III). In addition to the characters given in these tables, it should be added that some Marshallese males have a few maxillary teeth as in females. Furthermore, the heart in Marshallese males, though sometimes as far forward as in Hawaiian males, is often located as far back as in Hawaiian females.

The two meristic differences between males and females, which seemingly occur in both Hawaiian and Central Pacific specimens, must be dealt with in somewhat greater detail. There would seem to be little doubt about the validity of the average difference between the pore counts of males and of females (Table IV). However, if the pore counts of males, females, and immatures of different sizes are plotted against standard length (Fig. 3), it can be seen that the pore counts of the immatures increase with increasing length up to about 200 mm. and that the pore counts of the males agree with those of immatures of the same size. Perhaps, the hypothesis might be erected that pore count is related directly to size (regardless of sex) and that the lower pore counts of males are simply due to the fact that males are smaller than

TABLE III
CERTAIN FEATURES OF THREE CENTRAL PACIFIC FORMS OF MORINGUIDAE

| Sex and maturity | Locality and date | Stand- ard length (mm.) | Pig- men- tation sym- bol ^a | Eye diameter ^c | | Pectoral fin (in thou- sandths of S. L.) | | Caudal fin | Diameter of larger eggs (mm.) |
|------------------|-------------------|----------------------------------|--|------------------------------|----|---|---------------------|-------------|----------------------------------|
| | | | | A | B | Length | Width of base | | |
| Immature (♀?) | Bikini, 8/47 | 189 | 0 | 1.1 | 16 | 1.6 | 1.6 | Pointed | (None found) |
| " " | " " | 222 | 0 | 1.2 | 16 | 1.4 | 1.6 | Rounded | " " |
| " " | " " | 237 | 0 | 1.1 | 17 | 1.3 | 1.3 | Pointed | " " |
| " " | " " | 275 | 0 | 1.1 | 16 | 1.1 | 1.8 | Rounded | " " |
| " " | " " | 300 | 0 | 1.3 | 22 | 1.7 | 2.7 | " | " " |
| Maturing ♀ | " 8/46 | 213 | 1 | 3.3 | 45 | 7.5 | 4.7 | Subtruncate | 0.15 |
| " " | Samoa, 6/39 | 240 | 2 | 3.8 | 51 | 7.9 | 4.2 | Truncate | 0.15 |
| " " | Bikini, 8/46 | 258 | 1 | 2.7 | 37 | 5.8 | 3.5 | Subtruncate | 0.15 |
| " " | " 8/47 | 260 | 1 | 3.8 | 50 | 11.2 | 3.8 | Trilobed | 0.3 |
| " " | " 8/46 | 263 | 1 | 3.0 | 42 | 6.8 | 4.2 | Subtruncate | 0.15 |
| " " | " 8/47 | 280 | 1 | 4.3 | 56 | 11.4 | 3.9 | Trilobed | 0.2 |
| " " | Samoa, 6/39 | 282 | 2 | 5.0 | 65 | 12.4 | 3.9 | Bilobed | 0.5 |
| " " | " " | 290 | 3 | 4.8 | 64 | 11.0 | 3.4 | Trilobed | 0.5 |
| " " | Bikini, 8/47 | 314 | 1 | 3.8 | 56 | 10.5 | 3.5 | " | 0.25 |
| Maturing ♂ | " 8/46 | 125 | 1 | 8.0 | 69 | 24.0 | 9.6 | " | ... |
| " " | " " | 131 | 1 | 7.6 | 68 | 22.1 | 6.9 | " | ... |
| " " | " 8/47 | 132 | 1 | 7.6 | 74 | 21.2 | 6.1 | Bilobed | ... |
| " " | " 8/46 | 137 | 2 | 8.8 | 74 | 21.9 | 8.8 | " | ... |
| " " | " 8/47 | 140 | 1 | 7.1 | 69 | 18.6 | 5.0 | Trilobed | ... |
| " " | Guam, 1/46 | 159 | 2 | 9.4 | 84 | 22.0 | 9.4 | Bilobed | ... |

^a As contrasted with Table II, these specimens are arranged in order of their increasing standard length within sex categories. Pigmentation symbols are based on specimens which were in alcohol for 7-15 years and undoubtedly somewhat faded. 0 represents plain yellowish pigmentation; 3, blackish above and silvery below; and 1 and 2, intermediate color phases.
^b A = thousandths of standard length; B = thousandths of head length.

females. The following facts fall into line with such a hypothesis. It is known that the lateral line in fishes develops from front to rear. Therefore, if the lower pore counts of smaller specimens is due to incomplete development of the lateral-line system, the distance from the last lateral-line pore to the base of the tail should be a greater proportion of the standard length in small (less than 200 mm.) than in large specimens (over 200 mm.). This proves to be true. Our smallest Hawaiian specimen (102 mm.) has an unusually low pore count of 92, and an exceptionally high distance from the last pore to the tail, of 150 thousandths of the standard length. In males (Table IV) averaging 170 mm., the mean pore count is 98 and the distance from the last pore is 79 thousandths. In specimens over 200 mm. (Table IV) the mean pore count is about 106 and the lateral line to caudal distance about 55 thousandths of the standard length (48 thousandths in our females, 59 in our

immatures). Despite the general agreement between the above evidence and the hypothesis mentioned, it would seem inadvisable to pin too much faith in it because of the following, indirectly contradictory evidence.

It seemed to us that if, despite the difference in male and female pore counts, the number of vertebrae in the two sexes were the same, then the hypothesis that pore count increased with length up to 200 mm. would be on firm ground. However, male and female vertebral counts definitely differ⁴, as shown by Table IV. That there should be an increase in vertebrae with increasing standard length seems doubtful,

⁴ These counts are all based on X-rayed material. The X-ray technique did not prove entirely satisfactory here, and in about half the specimens the vertebrae could not be counted with certainty. Such specimens, which include all of the small immatures, have been omitted from the present data. The small specimens appear to have poorly ossified vertebrae, and all specimens tended to have kinks in more than one plane, some of which would lift parts of the specimen off the film and out of focus.

TABLE IV
VERTEBRAL AND LATERAL-LINE PORE COUNTS OF HAWAIIAN MORINGUIDAE

| Sex | Standard length (mm.) | Number of vertebrae | Pores from gill opening to end of lateral line | Vertebrae minus pores | Distance from ¹ last pore to base of tail in thousandths of S. L. |
|-----------------|-----------------------|---------------------|--|-----------------------|--|
| Maturing male | 156 | 120 | 95 | 25 | 102 |
| " " | 167 | 118 | 97 | 21 | 72 |
| " " | 174 | 120 | 95 | 25 | 91 |
| " " | 177 | 122 | 104 | 18 | 50 |
| Average | 168 | 120 | 98 | 22 | 79 |
| Maturing female | 265 | 130 | 101 | 29 | 68 |
| " " | 327 | 122 | 108 | 14 | 36 |
| " " | 346 | 127 | 106 | 21 | 44 |
| " " | 368 | 127 | 106 | 21 | 45 |
| Average | 320 | 126 | 105 | 21 | 48 |
| Immature | 219 | 127 | 105 | 22 | 50 |
| " | 220 | 126 | 108 | 18 | 50 |
| " | 235 | 128 | 107 | 21 | 64 |
| " | 245 | 127 | 106 | 21 | 61 |
| " | 247 | 127 | 106 | 21 | 61 |
| " | 261 | 128 | 107 | 21 | 69 |
| " | 321 | 128 | 106 | 22 | 65 |
| " | 408 | 127 | 105 | 22 | 54 |
| Average | 270 | 127 | 106 | 21 | 59 |

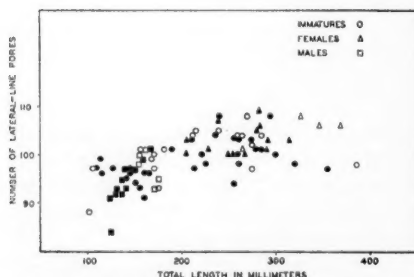


Fig. 3. Relationship between pore count and length in *Moringua*. Hollow symbols represent Hawaiian specimens; solid symbols represent U. S. National Museum specimens, mostly from the Marshall Islands, with a few specimens from Samoa and Guam.

though our present data are insufficient to prove that such an increase does not occur.

One of the purposes of making vertebral counts was to determine the extent of the correlation between vertebral and pore counts. There is, it appears, one pore per vertebra. The greater number of vertebrae than pores arises from the fact that there are several pores and vertebrae ahead of the point (over the gill openings) at

which we started our lateral-line counts and several more vertebrae behind the last lateral-line pore. Apparently the excess of vertebrae over pores is about the same in our males, females, and (large) immatures (Table IV). There is, however, a considerable individual variation in this excess; and as the pore count in eels seems to be a good indication of vertebral number (Gosline, 1951: 303), it is of some importance to know where this variation arises.

Our belief is that the individual variation in the difference between vertebral count and pore count stems primarily from the fact that in some individuals the lateral line extends somewhat farther back than in others. If this is correct, then the differences between vertebral and pore counts should be correlated with the distance (relative to standard length) between the last pore and the base of the caudal. The correlation coefficient for these features, in the specimens over 200 mm. in Table IV, is .60, indicating that such a correlation does exist. The low value of this figure, however, also indicates other sources of variability besides the backward extension of the lateral line as the

cause of the discrepancy between pore and vertebral count.

One might anticipate in moringuids, as in *Anguilla*, a certain amount of divergence at sexual maturity from an immature form in which the sexes were approximately similar. However, it seems most unlikely that our male moringuids ever passed through a stage similar to that of our immature females. For one thing, the head length of our males is relatively greater than it ever becomes in our females and immatures, and there is no indication that in females the head length increases at the onset of sexual maturity. (Though our data on this point have not been given here, the same thing is shown by Gordon, 1954, Table I, for the West Indian species). Second, the eye is larger than it ever becomes in our females. Third, that the generally more forward position of the male heart makes a change from the immature form into the adult male seems most improbable. It seems unlikely that in males the heart should undergo a backward displacement, such as is found in immatures, only to return toward its normal position with maturity, particularly as there is no such return movement in females.

We have examined all of our immature Hawaiian moringuids, especially the smaller specimens, to see whether any of them showed either the heart in the forward, male position or intermediate in location between the conditions found in males and females (and thus indicating some change in position with growth in males). No evidence for either of these possibilities was found. Consequently, the conclusions seem warranted that our immatures are all females, and that immature males have yet to be taken despite special efforts on our part to collect them.

Several factors point to the hypothesis that the immature form of our adult males more or less drastically curtails or totally omits the period of subterranean existence found in immature females. For one thing, although we have taken small but approximately equal numbers of maturing males and females and numerous immature females, we have apparently never, as stated, collected immature males. Second, the fact that immature, fossorial females from 102 to 415 mm. in length have been collected, but that our largest ripe male is only 183 mm. long, indicates at least

that the amount of growth in the subterranean phase of the male cannot be as great as that of the female. Last, certain features common to the fossorial stages of other moringuids are absent from our maturing and presumably from immature males, e.g., posterior heart position; this at least suggests a different mode of life for the immature male.

As to the question of whether or not our males belong to the same species as our females and immatures, no final proof can be given at this time. If they represent the same species, then this species shows a sexual differentiation that is almost unbelievable for fishes. If they represent a different species and genus, then some very peculiar circumstances remain to be explained. In the first place, where are the females of the species for which we have males and where are the males to correspond to our females? Why should the males of one species and the females and immatures of another be taken in the same habitat? (These same two questions have already been asked by Parr in relation to the two Atlantic forms discussed in footnote 3). We have never taken males in Hawaii without also taking immature females, and we have collected mature males and females and immatures from the same small section of a rotenone station. Again, (Table I) the ripening of the two sexes seems to occur at the same general season. Finally, the males, females, and immatures agree well in certain features such as the position of the anus, etc., and the ripening males and females agree in coloration. Because of all these considerations we provisionally prefer the hypothesis that our male, female, and immature moringuids all represent a single species. It would take only a single Hawaiian specimen, e.g., a female "*Anguillichthys*" or a male *M. abbreviata* type, to disprove this hypothesis, but so far we have looked for such a specimen in vain.

The name to be applied to our species remains to be discussed. As already noted, the names *M. abbreviata*, *M. macrocephala*, and *M. bicolor* as defined by Schultz all seem to be applicable to female and immature forms of our species. However, the oldest name available for it seems to be *Moringua macrochir* Bleeker, which Schultz (1953: 93) used primarily (but not entirely) for males of what we believe to be the same species. It is therefore *M.*

macrochir that we provisionally apply to all the forms we have been discussing.

COMPARISON WITH OTHER EELS

Though there appears to be only one moringuid in Hawaii, *M. macrochir*, there are certainly others elsewhere in the Central Pacific, e.g., in the Marshalls. We have not studied these in detail but it may be helpful to state our basis for differentiating them from *M. macrochir*. On the basis of the U. S. National Museum material, we have concluded that all the Central Pacific moringuids with the lower jaw protruding and with pore counts from 84 to 110 belong to *M. macrochir*.

Morphologically, the most aberrant form of the Hawaiian moringuid is the immature, worm-like, burrowing (female?). There are in Hawaii several eels belonging to other families that have taken up a similar habitat. Some of the salient biological features of two of these are compared with *M. macrochir* in Table V. In none of these is there any great sexual differentiation or external change with the onset of sexual maturity.

Finally the resemblances between the life histories of moringuids and anguillids should be noted. These two eel families seem to be about the only ones having members (apparently only one species in the Moringuidae) that habitually spend part of their lives in fresh water. These families are also the only ones to our knowledge in which certain species at least undergo very striking (and more or less parallel) changes in external morphology at the onset of sexual maturity. Both of these features suggest a genetic relationship between

the two families despite their rather different appearance. This suggestion is borne out by the osteology of the two families (Regan, 1912). If from this relationship one can gain some criterion concerning primitiveness in the family Moringuidae, then it is again the "*Anguillichthys*" form of moringuid represented by the males of our species that is the least specialized.

SUMMARY AND DISCUSSION

An attempt to identify the Hawaiian species of the eel family Moringuidae has led us into rather numerous and difficult problems. Some of these have been more or less satisfactorily solved; others remain wide open. To facilitate future work we present in this summary first those facets of the investigation for which a particular solution is rather strongly indicated, followed by those aspects for which interpretations become increasingly undocumented.

A more or less complete transition has been demonstrated between the small-eyed, yellowish, rudimentary-finned immature Hawaiian form and the larger-eyed, silvery, longer-finned adult female. The former has been identified among Marshallese specimens by Schultz (1953: 86) as *Moringua abbreviata*, the latter as *M. bicolor*; *M. macrocephala* of Schultz is a form ontogenetically intermediate between these two.

The morphological changes that occur with the onset of female sexual maturity seem to be associated with a change from a fossorial to a pelagic mode of life. Similar developmental differences are known to occur in *Anguilla*, but do not take place in Hawaiian fossorial eels other than *Moringua*.

TABLE V
MATURATION IN HAWAIIAN BURROWING EELS

| Family and species | Differences between maturing males, maturing females, and immatures | Ripening males | | Ripening females | |
|----------------------------------|---|----------------|------------------|------------------|------------------|
| | | Number | Size range (mm.) | Number | Size range (mm.) |
| Moringuidae | Great | 8 | 155-183 | 5 | 265-368 |
| <i>Moringua macrochir</i> | | | | | |
| Opichthidae | None | 3 | 280-305 | 12 | 285-355 |
| <i>Caecula platyrhyncha</i> | | | | | |
| Muraenidae | None | 4 | 220-330 | 7 | 235-305 |
| <i>Uropterygius marmoratus</i> * | | | | | |

* This species inhabits rocky areas and is less strictly a fossorial form than the other two.

Passing to those features of the investigation for which our evidence is less secure, we believe that our mature Hawaiian males represent the same species as our females and immatures. Marshallese males corresponding to the Hawaiian males have been identified by Schultz as *Moringua macrochir*. Morphological differences similar to those between Hawaiian males and females occur in the West Indian moringuids. These differences include such features as heart position and vertebral count, as well as a number of less important characters.

Third, there remain the problems for which we have at present no answers. First, where are the immature males? Despite serious effort, we have been unable to show any transition between any immatures and the mature male form. Because our immatures resemble the maturing females far more than the males, we have provisionally identified all of our immatures as undeveloped females. Also, why does such a great morphological difference exist between the sexes in our moringuids when the males and females of other Hawaiian eels are strikingly similar? In an attempt to provide an answer to the above two questions, we have suggested the working hypothesis that the males may rather drastically curtail or omit the immature fossorial and morphologically specialized stage found in females.

Another unsolved problem arises from the sizes of immature females. From all of the stations at which we have taken maturing females, we have also taken specimens, showing no signs of maturity, that are larger than our largest mature forms. There would seem to be at least three possible answers to this problem, i.e., that the large immatures are sexually abnormal, that they are out of phase with the spawning cycle of the smaller maturing females, or that they represent a different species. Regarding the third possibility, we can find no morphological differences between the large immatures and smaller ones. Regarding the second, we have at least the evidence that female maturity in Hawaii occurs at various sizes from 265 to 365 mm. This would throw no light on the problem of our very large immatures if our moringuids spawned more than once. But it seems more likely that our Hawaiian moringuids, like *Anguilla*, spawn once

and die. Perhaps the same reason why some of our females mature at 265 mm. and others at 343 mm. will explain why still others remain immature at 415 mm. In any event, there is no strict correlation between either size and female maturity or size and female immaturity.

Finally, we find in the Hawaiian vs. Marshallese moringuids a problem held in common with many other fishes (Gosline, 1955: in press). In Hawaii, moringuid spawning appears to occur only in winter; in the Marshalls it takes place in the same species in the summer and presumably all year around. If moringuids are basically tropical fishes, as everyone assumes they are, then one would expect them on moving into the colder Hawaiian waters to restrict the spawning period to the warmest, not the coldest months (Ekman, 1953: 113). The reversal of the expected spawning period in Hawaiian waters remains unexplained for *Moringua* as for many other fishes.

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Description of the Lateral-line System of the Pirate Perch, *Aphredoderus sayanus*¹

GEORGE A. MOORE AND WILLIAM E. BURRIS

THE lateral-line system of *Aphredoderus sayanus* (Gilliams) apparently has never been studied in detail. The remarkable development of cutaneous sense organs in this singular species seems to have been almost entirely overlooked.

In taxonomy the term lateral line usually refers to that part of the system called the lateral canal (Hubbs and Cannon, 1935), which lies along the sides of the fish from the upper angle of the gill cleft backward. The extent of development of the "lateral line" evidently is subject to considerable variation in the pirate perch since Baker (1939) stated there is "no lateral line" and Jordan and Evermann (1896) described it as "imperfect or wanting." Regan (1911) ascribed a complete lateral line to the order Salmoperca, which includes the pirate perches and the trout perches (*Percopsis* and *Columbia*). Regan gave a brief description of the "muciferous channels" on top of the head.

In our specimens (*A. s. gibbosus* LeSueur), the lateral canal extends from the upper angle of the gill cleft to a point below or slightly behind the dorsal origin. The lateral canal is continuous anteriorly, bearing a pore near the posterior border of each scale. Caudal from this continuous canal a few scales bear short tubes, open at each end. In all there are 13 to 18 pored scales in the lateral canal. Careful examination reveals the presence of neuromasts on most scales behind the tubular portion. These naked organs, not in tubes, are devoid of pigment cells

and therefore may be readily seen in the usual position of the "lateral line."

The material for this study included 110 specimens (52 to 113 mm. in standard length) collected by means of rotenone from Subprison Lake, 4 miles north of Stringtown in Atoka County, Oklahoma, by Gordon E. Hall on December 13, 1950.

The lateral-line system was studied in various ways as follows: injection of the canals with india ink; dissection; microtome sections, cut from tissue blocks embedded in celloidin, and stained with Mallory's connective tissue stain and haematoxylin and eosine; skins stained with borax carmine; and by means of a binocular microscope and an air jet.

Large specimens present to the unaided eye a conspicuous pattern of cutaneous organs (Fig. 4) in transverse rows on each side of the middorsal line of the head and in vertical rows on the sides of the head, opercles and mandibles (Pl. I). Most scale pockets also bear a vertical row of organs situated on the exposed posterior fields. Anteromesad to each of the anterior nostrils there is a large cluster of organs somewhat greater in diameter than the nostrils. Upon close examination each of these clusters is seen to be composed of about 80 separate papillose neuromasts closely matted together. Since some of the papillae are actually composed of 2 or 3 neuromasts, a prenasal cluster probably includes about 100 functional units. Posterior from the prenasal clusters, and on each side of the middorsal line, the interorbital and snout regions bear about 12 irregularly and diagonally placed rows each containing 12

¹ Contribution No. 51 from the Research Foundation and No. 236 from the Department of Zoology, Oklahoma Agricultural and Mechanical College, Stillwater.

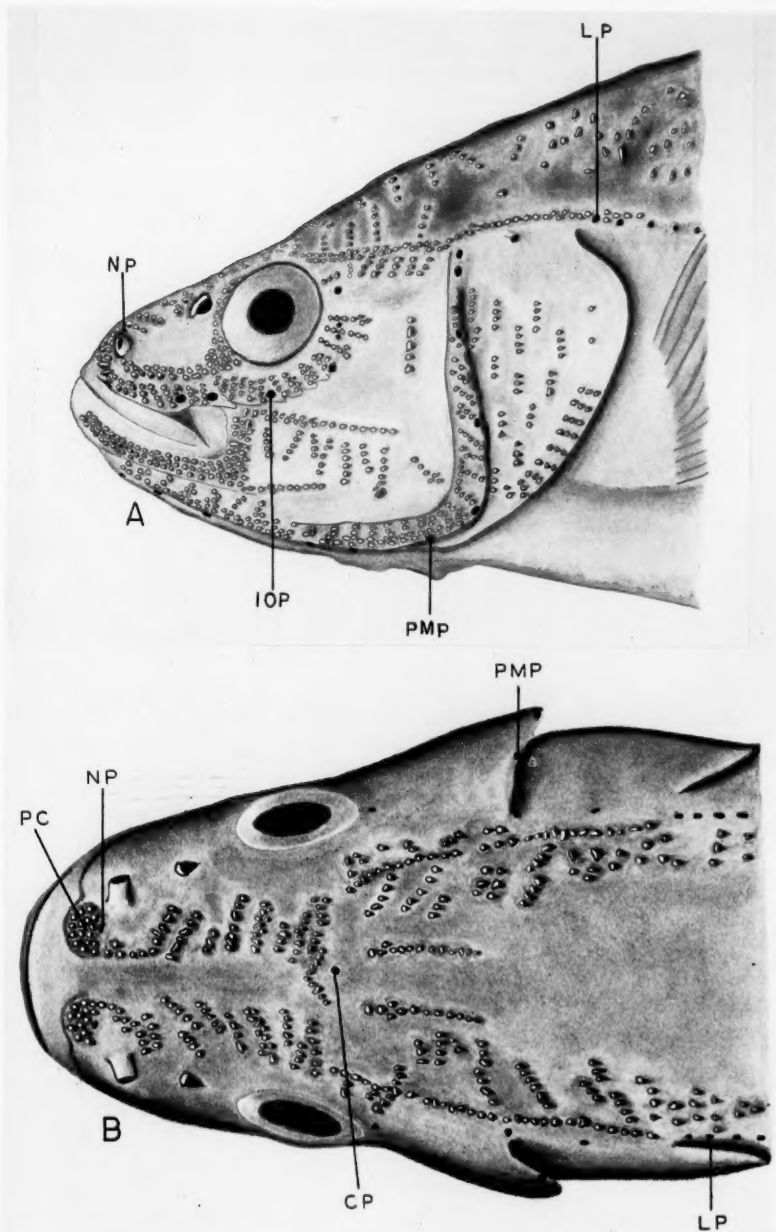


PLATE I

The cephalic sensory areas of *Aphredoderus sayanus*: A—lateral view of head; B—dorsal view.

Drawings made from photographs with the aid of a pantograph. Because of representational difficulties with the medium used, the number of superficial neuromasts shown in a given area is much fewer than in the equivalent area of the specimen. Scales were omitted.

Abbreviations: CP, coronal pore; IOP, infraorbital pore; LP, lateral-line pore; NP, nasal pore; PC, pre-nasal cluster; PMP, preoperculo-mandibular pore.

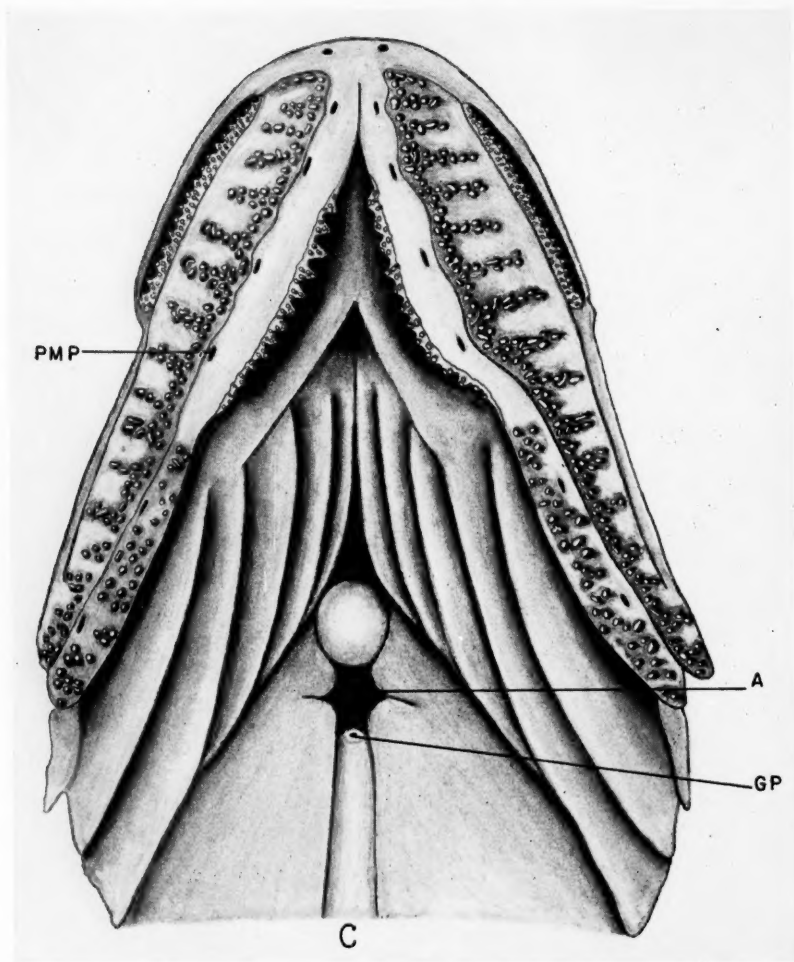


PLATE II

The cephalic sensory areas of *Aphredoderus sayanus*: C—ventral view of the head.
Abbreviations: A, anus; GP, genital pore; PMP, preoperculo-mandibular pore.

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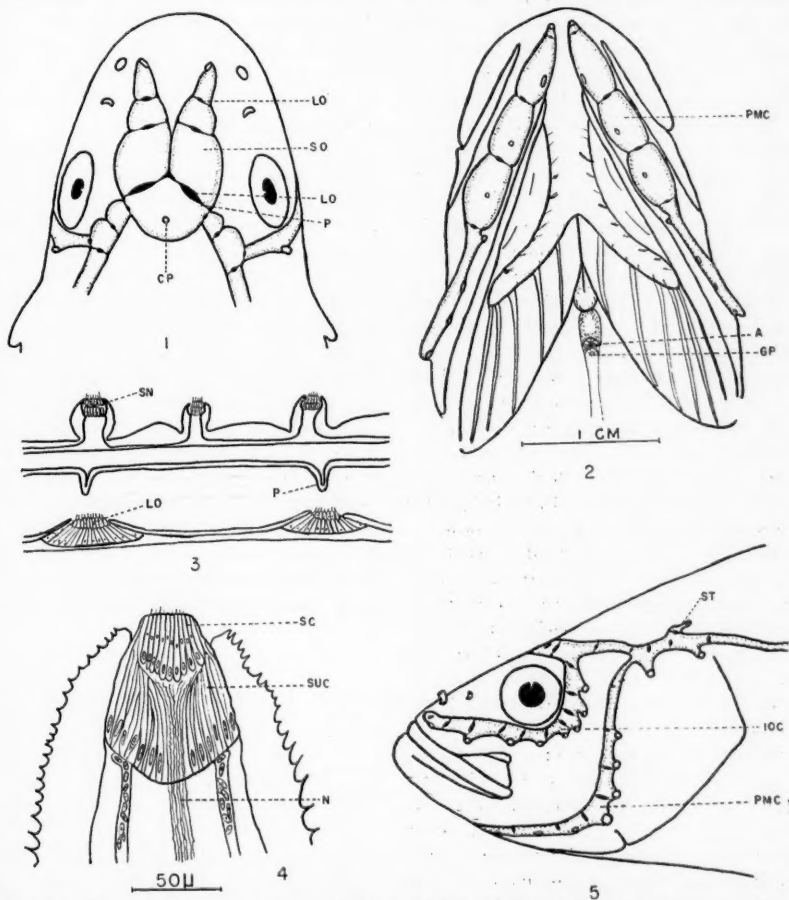
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to 25 papillae. Behind the coronal pore on each side of the median line of the nape a longitudinal row of papillae extends about one-third the distance to the dorsal origin. Still another row extends horizontally from the orbit and slightly above the upper angle of the gill cleft to the lateral canal (Pl. I, A, B).

Extending downward along the upper half of the anterior orbital rim is a band of organs that bends forward at right angles from the mid-

anterior orbital rim to a point below the anterior nostril. Below this line of organs and lying over the lacrimal-suborbital series of bones, are about 15 vertical rows of papillae (Pl. I, A).

Three groups of organs are located on the mandible below the lower lip. Along the upper edge of the mandible there is a complex mat of organs in 5 or 6 rows closely set on the edge of a flap-like evagination of the integument. On the skin covering the mandibular ramus of the



Figs. 1-5. Diagrammatic aspects of the cephalic lateral-line system of *Aphredoderus sayanus*. Fig. 1—dorsal aspect of the head; Fig. 2—ventral aspect; Fig. 3—longitudinal section of the mandibular ramus of the preoperculomandibular canal showing two canal organs and three of the numerous superficial neuromasts; Fig. 4—enlargement of a superficial neuromast (drawn with the aid of a camera lucida); Fig. 5—lateral aspect of the head.

Abbreviations: A, anus; CP, coronal pore; GP, genital pore; IOC, infraorbital canal; LO, lateral-line organ; N, branch of lateral line nerve; P, partial partition in lateral-line canal; PMC, preoperculomandibular canal; SC, sensory cell; SN, superficial neuromast; SO, supraorbital canal; ST, supratemporal canal; SUC, supporting cell.

preoperculomandibular canal there is another band of organs in 3 or 4 rows from which lateral series extend outward at right angles. On the inner edge of the mandible there is a row of smaller clusters of 5 or 6 organs each (Pl. II, C).

The major bands of superficial neuromasts are situated over the lateral-line canals (Hubbs and Cannon, 1935), all branches of which are represented although the supratemporals (Fig. 5) are reduced to short branches extending upward from the lateral canals and bearing a small pore which is difficult to see. The supraorbital canals open anteriorly in the nasal pores and coalesce posteriad in a large chamber (Fig. 1) with the coronal pore (double in one specimen) in its roof. The infraorbital canal is complete with usually 7 (extremes 6 to 10) pores, which open at the ends of short branches below the canal, and connects with the lateral canal directly above the posterior margin of the orbit (Fig. 5). The preoperculo-mandibular canal has 9 to 12 pores which open on the canal or on short side branches. Two short branches of the lateral canal open in pores on the upper opercular margin.

The lateral-line organs in the canals are large and barely visible to the unaided eye. One organ measured 791 microns in length and 264 microns in width. Each organ, on surface view, is spindle shaped and lies with its long axis at right angles to the canal axis. Its central portion is slightly elevated to present a fusiform, cushion-like appearance (Fig. 3). Around this elevation there is a shallow moat-like groove. The elevated portion is the exposed surface of the sensory-cell group, although near the edge of the groove some of the supporting cells reach the surface.

The sensory canals are relatively large (Figs. 1, 2, and 5). The supraorbital canal and the mandibular portion of the preoperculomandibular canal are much larger in diameter and depth than the other cephalic canals. The canals are provided with constrictions which occur adjacent to the location of each sense organ and thus divide the canals into linear series of compartments. These compartments connect with each other by an aperture through a velum-like partition composed of a flap of tissue continuous with the lining of the canal (Fig. 3). The diameter of the canal lumen is, therefore, greatly lessened at the location of each organ.

The canal organs are structurally similar to

the superficial neuromasts, but much larger. As usual in fishes, the lateral-line organs consist of a bundle of sensory cells, each provided with a single sensory hair and the whole bundle couched in a group of supporting cells penetrated in the center by a branch of the acustico-lateralis nerve (Fig. 4). Blood capillaries penetrate the organ between the supporting and sensory cells.

The lateral-line system is known to be receptive of vibratory stimuli which make it possible for fishes to detect food organisms in the dark, the presence of enemies, the nearness of objects, members of their own species (in schooling and spawning), and in maintaining position in a stream (Wunder, 1936).

We are not aware of any published descriptions of lateral-line systems in which partitions, similar to those above-mentioned are treated. However, Moore (in Press) is describing similar structures and other unusual features of the cephalic canals of *Lepomis humilis* (Girard).

Although experimental data are lacking, we venture to postulate the following explanations of the function of the velum-like partitions. Vibrations set up in the water, sufficiently near the fish, strike the epithelial covering over the canals and also enter the canals by way of pores. The outer canal walls may act as amplifiers to transmit vibrations to the fluid in the canals. Vibrations thus set up in the canals would tend to be intensified in the immediate vicinity of the sensory endings of the lateral-line organs since those organs are situated at the critical points where the canal lumens have their least diameter.

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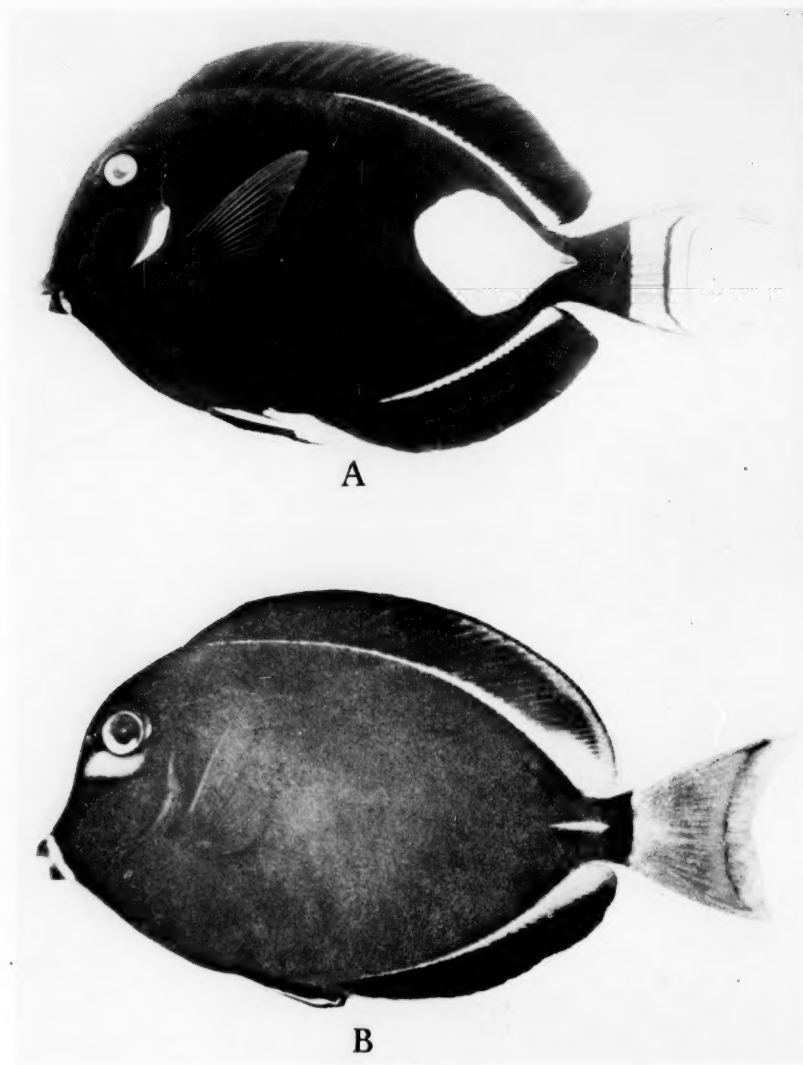


PLATE I

A—*Acanthurus achilles*. Reproduced from a 35-mm. Kodachrome transparency of a 170-mm. specimen from the Hawaiian Islands.

B—*Acanthurus glaucopareius*. Reproduced from a 35-mm. Kodachrome transparency of a 112-mm. specimen from the Gilbert Islands.

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Acanthurus rackliffei, a Possible Hybrid Surgeon Fish (*A. achilles*
 \times *A. glaucopareius*) from the Phoenix Islands

JOHN E. RANDALL

THE published records of naturally occurring hybrids of freshwater fishes are very numerous; those of marine fishes are exceptionally few in number. In an unpublished review of hybridization in New World fishes, Robert Rush Miller advises me that only 5 marine hybrids have been reported (1954) in contrast to 129 freshwater crosses. Only one additional instance of hybridization in marine fishes has come to his attention since this list was prepared. The overwhelming majority of freshwater hybrids is reflected not only from our greater knowledge of American freshwater fishes and greater opportunity for sampling populations of freshwater habitats but probably also from an actual lower percentage of hybrids in the sea. Undoubtedly conditions are more favorable, in general, for hybridization of fishes in the freshwater environment than in the marine.¹

Acanthurus rackliffei (Schultz, 1943: 157, 163, fig. 13) is known from three specimens, each collected in a different locality (a pool on the reef, the outer edge of the reef, and the channel connecting the ocean to the lagoon) at Hull Island, an atoll in the Phoenix Islands, Oceania. Admittedly three specimens are too few on which to base evidence of hybridization, but the intermediacy of these between *Acanthurus achilles* Shaw and *Acanthurus glaucopareius* Cuvier is such that their hybrid nature appears probable. Also, in view of the above-mentioned paucity of records of hybrid marine fishes, even suspected cases are well worth documenting.

I know of no reference to hybrid surgeon fishes. The marine hybrid closest from a phylogenetic standpoint is an example in the Chaetodontidae from Tortugas, Florida, cited by Longley (in Longley and Hildebrand, 1941: 154). He concluded that *Holocanthus townsendi* (Nichols and Mowbray) was probably a cross between *H. ciliaris* and *H. isabelita*.

Acanthurus achilles (Pl. I A) is a strikingly colored fish, dark purplish black in life with a

large elliptical bright orange spot posteriorly on the body. At the rear this spot has a characteristic sharp, folding spine. The spot has been cited as an example of warning coloration in fishes. Similar, but apparently independently acquired, bright color around caudal spines of *Acanthurus monroviae* Steindachner, *Naso lituratus* (Schneider) and *Naso unicornis* (Forskål) supports this contention. *A. achilles* is abundant in the oceanic islands of the tropical Pacific. Günther (1861: 340) recorded it from China. It is not known from the East Indies, and there is but one questioned reference to it from the Philippines (Elera, 1895: 532). Herre (1927: 414, pl. 2, fig. 1) included it in his report on Philippine surgeon fishes only on his belief that it occurred in the Philippine Islands. His specimen was from Guam.

Acanthurus glaucopareius (= *aliala* Lesson) (Fig. 1 C) is also dark but lacks the orange spot. This species has an oval white area beneath the eye and bright yellow coloration at the base of the dorsal and anal fins. It is an even more wide-ranging species, known from the entire tropical Pacific, and is one of the few surgeon fishes to have crossed the eastern Pacific barrier (Ekman, 1935: 105), being recorded from the Galápagos Islands, Cocos Island, Clipperton Island, and the Revillagigedo Islands. It does not appear to be present in the Indian Ocean except for Christmas and Cocos-Keeling Islands.

These two species, along with *Acanthurus leucosternon* Bennett, from the East Indies and tropical Indian Ocean, are closely related. They share a number of characteristics that separate them from other species of *Acanthurus*. They are high-bodied, and the profile of the head is steep and convex; the mouth is somewhat produced and very small (its width from rictus to rictus is contained about 5 to 6 times in the length of the head, as opposed to 3.2 to 4.8 for other species); the teeth are large, few in number (never over 12 in either jaw), and different in shape from other surgeon fish (see Aoyagi, 1943, pl. 6, fig. 19 for drawing of teeth of *glaucopareius*); dorsal and anal fin-

¹After this paper was in press, a comprehensive article on the natural hybridization of fishes appeared (Hubbs, 1955). The reader is referred to that work for a more detailed discussion of hybridization in marine fishes.

ray counts are high; there is a white line on the chin adjacent to the lower lip; the size of *achilles* and *glaucofareius* (that of *leucosternon* not seen) at transformation from the acronurus or late postlarval stage to the juvenile form is very large, about 55 to 60 mm. in standard length. The largest of numerous examples at transformation of all of the other species of *Acanthurus* that I have examined is 38 mm., and some are as small as 18 mm. The sum total of these characters would be of sufficient magnitude to warrant consideration of these three species as a subgenus, were it not for *Acanthurus pyroferus* Kittlitz (= *celebicus* Bleeker) (= *leucosternon* Fowler and Bean, Aoyagi, and Schultz and Woods), which serves as a connecting link to more typical forms of *Acanthurus*.

The similarity of *achilles* and *glaucofareius* is not restricted to morphology, but carries over to habitat and to their herbivorous food habits. On the outer reef, windward side, of Onotoa Atoll in the Gilbert Islands, *achilles* was most characteristic of surge channels, not the surf zone where *Acanthurus guttatus* is the index form, but the outer, somewhat less turbulent part. *A. glaucofareius*, though seen in surge channels and elsewhere in the atoll, was most abundant on the inshore part of the

coralliferous terrace. These two regions of the reef are not sharply demarcated from one another, and there is a broad overlap of the zones occupied by the two species; they were frequently observed swimming side by side. Harry (1953: 150) stated that *glaucofareius* (his *Acanthurus sp. one*) was often in association with *Acanthurus achilles* at Raroia Atoll, Tuamotu Archipelago. The stomach contents of 10 specimens of *achilles* and 12 of *glaucofareius* from Hull and Enderbury Islands in the Phoenix group were examined and found to be essentially the same in both species. Most of the algae was fine and filamentous, and very little sedimentary material was present. No single alga predominated, although there were more reds in general, such as *Alsidium* sp., *Gelidium* sp., and *Lophosiphonia* sp. than greens, browns, or bluegreens. More *Caulerpa serrulata*, a green alga common on the outer part of the reef flat, was found in *achilles* stomachs, probably reflecting the greater tendency on the part of this species to enter shallow water. (Algal determinations by M. Doty and M. Bell, University of Hawaii.)

Nothing is known of the breeding habits of either species. The gonads of 36 adult specimens of *achilles* and 27 of *glaucofareius*, collected from May to September in the Phoenix,

TABLE I

COMPARISON OF COLOR AND MORPHOLOGY OF *Acanthurus achilles*, *Acanthurus glaucofareius*, AND HYBRID

| Character | <i>achilles</i> | <i>achilles</i> × <i>glaucofareius</i> | <i>glaucofareius</i> |
|---|---|--|--|
| Shape of caudal fin | Strongly lunate | Moderately lunate | Emarginate |
| Dark submarginal line in caudal fin | Present and prominent | Present | Faint and narrow |
| Demarcation of dark body color and pale color of caudal fin | Located at base of caudal fin | Located $\frac{1}{8}$ caudal length distal to base of caudal fin | Located $\frac{2}{8}$ caudal length distal to base of caudal fin |
| Pale area around and in front of caudal spine of adults | Large | Small | Absent |
| Pale area at base of posterior dorsal and anal fin rays | Narrow, about $\frac{1}{4}$ length of last few rays | Moderately broad, about $\frac{1}{2}$ length of last few rays | Broad, about $\frac{3}{8}$ length of last few rays |
| Color and width of middle part of opercular membrane | White and broad | Dark and narrow | Dark and narrow |
| Pale spot under eye | Absent | Faint, maximum height $\frac{1}{2}$ eye diameter | Large and conspicuous, maximum height $\frac{2}{3}$ eye diameter |
| Pale mark on chin | Ends at rictus | Ends at rictus | Extends above rictus |

TABLE II

FIN-RAY COUNTS OF *Acanthurus achilles*, *Acanthurus glaucopareius*, AND HYBRID

| Species and locality | Dorsal soft rays | | | | | Anal soft rays | | | | |
|--|------------------|----|----|----|----|----------------|----|----|----|----|
| | 28 | 29 | 30 | 31 | 32 | 33 | 26 | 27 | 28 | 29 |
| <i>achilles</i> | | | | | | | | | | |
| Phoenix Islands..... | | 1 | 3 | 5 | 2 | .. | .. | 3 | 6 | 2 |
| Oceania..... | | 7 | 28 | 53 | 32 | 2 | 3 | 25 | 56 | 38 |
| <i>achilles</i> X <i>glaucopareius</i> | | | | | | | | | | |
| Phoenix Islands..... | | 1 | 1 | 1 | .. | .. | .. | 2 | 1 | .. |
| <i>glaucopareius</i> | | | | | | | | | | |
| Phoenix Islands..... | 1 | 3 | 6 | 2 | .. | .. | 3 | 9 | .. | .. |
| East Indies, Oceania, and Galapagos Islands..... | | | | | | | | | | |
| | 8 | 30 | 31 | 6 | .. | .. | 19 | 48 | 8 | .. |

Gilbert, and Marshall Islands, were found to be in all stages of development and no trend could be perceived over this period. Occasional specimens of both species, collected at the same time, had comparably developed gonads. Study of a much larger number of adult *Acanthurus triostegus* from Pacific islands of the lower latitudes revealed ripe fish throughout the year. It is believed that there is no definite spawning season for these fishes in these regions. This might be expected from the very slight annual variation in water temperature.

A. achilles and *A. glaucopareius* may be separated primarily by caudal-fin shape, a slight difference in number of dorsal and anal fin rays, and by color (Tables I-II). It will be noted that the postulated hybrid either shares color characters of *achilles* or *glaucopareius* or is intermediate. Fig. 1 shows the posterior parts of specimens of about equal size of all three forms from Hull Island. The illustration of the hybrid is drawn from the paratype of *rackliffei* in the Museum of Comparative Zoology, Harvard College. The holotype and a small paratype are in the United States National Museum. There appears to be a progressive development of the pale area around the caudal spine in the three specimens of *rackliffei*. It is absent in the 68-mm. paratype, narrowly developed in the 150-mm. holotype, and obvious in the 161-mm. paratype, as figured. In *achilles* there is a similar enlargement of the pale area around the spine with

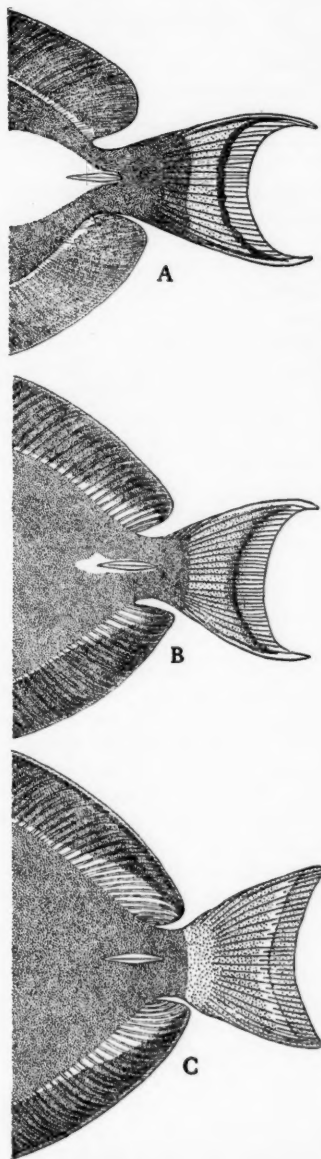


Fig. 1. Caudal regions of: A—*Acanthurus achilles*, B—*Acanthurus rackliffei* (*achilles* X *glaucopareius*), and C—*Acanthurus glaucopareius*, all from Hull Island. Standard length 158 to 161 mm. Drawing by L. B. Isham, United States National Museum.

age, although it takes place over a much shorter range in standard length and is first visible at a smaller size (about 65 to 70 mm.). The absence of the orange spot in the young led Günther (1873: 114, pl. 77, fig. B) to err in describing a juvenile *achilles* as a new species, *Acanthurus aterrimus*. Schultz (1943: 162) should be credited as the first to recognize the identity of the two.

Although I have indicated in Table I that the pale chin mark does not extend above the rictus in the hybrid, it does so very inconspicuously in the 161-mm. specimen.

A definite difference can be seen between the counts of the soft rays of the dorsal and anal fins of *achilles* and *glaucopterus*, but an overlapping exists. The counts for the three hybrids are about as intermediate as they could be, but it is apparent that many more specimens are needed to indicate where the modes of fin-ray counts lie.

Gillraker counts are not useful in effecting a separation of *achilles* and *glaucopterus*, for they vary from 16 to 20 in both species. The holotype of *rackliffei* has 18 anterior and 19 posterior rakers on the first gill arch.

On two extremes of its range, *Acanthurus glaucopterus* has color phases which co-exist with the normal. Schmidt (1930: 102, pl. 6, fig. 3) described one as a subspecies (*Hepatus aliala japonicus*) from the Riu Kiu Islands. The most conspicuous feature is the white area beneath the eye. Instead of being restricted to the region immediately below the eye, it consists of a broad band that runs from the eye to the mouth. Aoyagi (1943: 210) reported on specimens from the Riu Kius that presented a series of color variants from *glaucopterus* proper to the *japonicus* form. Marshall (1950: 194) and Palmer (1950: 202) recorded a color form from Cocos-Keeling Islands and Christmas Island, respectively, which differs principally from the usual type in lacking a sharp demarcation between the dark body color and the pale caudal fin; instead, the two colors gradually merge over the proximal third of the fin. In addition the ground color of the dorsal and anal fins is a good deal lighter than that of normally colored specimens. Apart from color, no significant distinction could be made by either author. Were it not for the decidedly more lunate

caudal fin, possible difference in fin-ray counts, and the similarity to *achilles*, one might consider *rackliffei* as another color phase of *glaucopterus*.

The possibility that *rackliffei* might be a valid species, fortuitously intermediate between *achilles* and *glaucopterus* cannot be discounted; however the latter two are common and *rackliffei* is rare—just as one would expect a marine hybrid to be (Schultz and Smith, 1936: 203). Also *achilles* and *glaucopterus* are so much alike that one might predict, *a priori*, that they would interbreed. Randall (MS) has succeeded in artificially fertilizing the eggs of *Acanthurus triostegus* from the Hawaiian Islands (although the larvae failed to develop past the sixth day). It might be possible to test the interfertility of *achilles* and *glaucopterus* in a similar way. Unfortunately this is not practicable in Hawaii, where *glaucopterus* is exceedingly rare. In the rest of Oceania *glaucopterus* is more abundant, and such an experiment could more readily be carried out.

The discovery of *rackliffei* in localities where either *achilles* or *glaucopterus* does not occur would be justification for rejecting the hypothesis of hybridization. *A. achilles* is recorded among the surgeon fishes of Wake Island (Fowler and Ball, 1925: 18; Fowler, 1940: 781), but *glaucopterus* is not. A week of extensive collecting and underwater observation at Wake Island by William A. Gosline and myself yielded no specimens of *glaucopterus*; however, *achilles* was extremely common. At Marcus Island Bryan and Herre (1903: 134) listed *achilles* but not *glaucopterus*. It is possible that the latter species is not present at these two outposts of Oceania. *A. achilles* appears to be absent from the following areas where *glaucopterus* is known to occur: Christmas Island and Cocos-Keeling Islands in the Indian Ocean, East Indies, Philippine Islands, Riu Kiu Islands, and islands of the tropical eastern Pacific. Admittedly the absence of a species from an area where it could logically occur is difficult to demonstrate. It was many years before *glaucopterus* turned up among the large fish collections made in the Hawaiian Islands.

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Growth, Dispersal and Survival of the Pacific Tree Frog

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THE amount and rates of growth and the length of survival in Amphibia are frequently estimated by the use of age groups established by examination of preserved specimens. Such studies are subject to considerable difficulties and the estimates obtained from them are often conflicting and inconclusive. Only a few field studies of this problem have been made with frogs. Ryan (1953) reviewed the studies on growth in *Rana* and presented additional data from the

study of marked individuals of *Rana clamitans*, *Rana pipiens* and *Rana catesbeiana*. Blair (1953) discussed some of the previous studies on *Bufo* and presented data on the growth of marked individuals of *Bufo valliceps*. Jameson (in press) studied the growth of the terrestrial cliff-frog *Syrnophorus marnocki*. The present study adds the Pacific treefrog, *Hyla regilla* to the species of Salientia that have been studied in nature by the use of marked individuals.

METHODS

Each frog was marked with a separate number by toe clipping. The method of marking, as well as certain aspects of the population structure and homing behavior in this tree-frog are discussed in a separate paper (Jameson, in press). Each of the 373 frogs marked and released in 18 collecting nights in or near a permanent pond in Washington County, Oregon, in 1953 was measured with a vernier caliper. Thirty-eight of these frogs were recovered in 3 collecting nights in 1954 and were remeasured. Early in the summer of 1953, 1,156 just-transformed juveniles were marked in a temporary pond in Washington County. The surrounding area was carefully worked during July and August to find how far the juveniles dispersed. Each individual was measured each time it was captured. The pond was collected twice in 1954 to determine if these individuals return to the pond where they hatched and to attempt to determine further survival and growth rates.

GROWTH

Growth in 38 male individuals of *Hyla regilla* from 1953 to 1954, as demonstrated by increase in snout-vent length, was much more rapid in smaller individuals than in larger ones (Table I). The smallest frog marked was 24.5 mm.; the longest, 43.9. The data suggest that only occasional individuals survive more than 3 years in nature or that once breeding size is

reached the individuals grow very little. No females were recovered.

Thirty of the 1,156 just-transformed individuals that were marked in order to study juvenile dispersal were recovered from 2 to 8 weeks following their original marking. The smallest just-transformed frog measured was 12.1 mm.; the largest, 15.3; the average size was 13.8. The 30 juveniles recovered in July and August of 1953 grew from 4 to 11 mm., with an average growth somewhat less than 2 mm. per week. Two of the 30 juvenile frogs known to survive one week were recovered in April, 1954 where they were part of a breeding chorus in the same pond. They were both males and were 29.4 and 32.6 mm. in length. (Table II).

JUVENILE DISPERSAL

In June, July and August of 1953 a small, temporary pond was utilized for a study of juvenile habits and dispersal. The area around the pond was well littered with cover (boards, logs, debris), and there were many boards close to the pond under which the just-transformed individuals could find moisture. These boards were utilized as traps, and 1,156 individuals were captured, measured, marked and released

TABLE I
ONE YEAR'S GROWTH (IN MM.) IN 38 ADULT
Hyla regilla

| Number marked, 1953 | Snout-vent length, 1953 | Snout-vent increment, 1954 | Average increase |
|---------------------|-------------------------|----------------------------|------------------|
| 10 | 26.0-27.9 | ... | ... |
| 13 | 28.0-28.9 | 10.2-11.4 (4) | 10.80 |
| 18 | 29.0-29.9 | 6.5-10.0 (5) | 8.65 |
| 21 | 30.0-30.9 | 6.0-11.9 (9) | 7.63 |
| 30 | 31.0-31.9 | 4.2-7.7 (7) | 6.19 |
| 34 | 32.0-32.9 | ... | ... |
| 45 | 33.0-33.9 | 4.7-7.2 (6) | 5.85 |
| 58 | 34.0-34.9 | 3.9-5.6 (6) | 4.80 |
| 52 | 35.0-35.9 | 4.2 (1) | 4.20 |
| 79 | 36.0-39.9 | ... | ... |
| 5 | 40.0-43.9 | ... | ... |

TABLE II
SNOUT-VENT INCREASE (IN MM.) OF 30 MARKED
JUVENILES OF *Hyla regilla*

Upper figure in each group is length of each just-transformed individual at time of marking; figure immediately below is length of the same individual at time of recapture

| Week when recovered | Week when marked | | | | | | | |
|---------------------|------------------|------------|----------------|--------|-----|-------|------|-----|
| | June | | July | | | | Aug. | 1st |
| | 3rd | 4th | 1st | 2nd | 3rd | 4th | | |
| July | | | | | | | | |
| 2nd | ... | 12 | ... | ... | ... | ... | ... | ... |
| | ... | 18 | ... | ... | ... | ... | ... | ... |
| 3rd | 12, 13, 13 | ... | ... | ... | ... | ... | ... | ... |
| | 19, 23, 23 | ... | ... | ... | ... | ... | ... | ... |
| 4th | 13 | 13, 13, 15 | 13 | 14 | ... | ... | ... | ... |
| | 24 | 17, 20, 20 | 23 | 19 | ... | ... | ... | ... |
| Aug. | | | | | | | | |
| 1st | 13, 14, 14 | 14, 14, 14 | ... | 14, 15 | 15 | ... | ... | ... |
| | 24, 20, 21 | 20, 21, 22 | ... | 19, 21 | 21 | ... | ... | ... |
| | ... | ... | 14, 14 | ... | ... | 14 | ... | ... |
| 2nd | ... | ... | 22, 22 | ... | ... | 20 | ... | ... |
| | 15 | 15 | 13, 13, 14, 14 | ... | ... | 15 15 | ... | ... |
| 3rd | 21 | 23 | 23, 23, 20, 22 | ... | ... | 25 21 | ... | ... |
| Total recovered | 8 | 8 | 7 | 3 | 1 | 2 | 1 | 1 |
| Total marked | 225 | 216 | 179 | 127 | 163 | 153 | 41 | ... |

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| 163 | 153 | 41 |

(Table II). A considerable number of the frogs marked in the first two weeks had probably transformed earlier. More time was spent in July and August to recover the juveniles which had dispersed than to mark new frogs at the edge of the pond. It is felt that only about one-fourth of the transforming tadpoles were marked. Twenty-three frogs were recovered within 100 yards of the pond, six from 100 to 200 yards and one frog was recovered 260 yards away. A part of the lack of recoveries may have been due to predators. Additional lack of recoveries may have been due to the juveniles seeking cover under one of the several houses in the vicinity, or of their going deep into the ground under logs. The cover was carefully turned and replaced, and digging was not attempted. Every precaution was taken to avoid the destruction of habitat.

The pond was collected in April, 1954 and 42 adults were removed. Seventeen of these were small enough to be definitely considered the previous summer's hatch, but only two of these showed evidence of having been marked. The area was visited again in May when it was found that the pond had been filled.

DISCUSSION

The growth of the Pacific treefrog is apparently very rapid during the first summer, the individuals almost doubling in length in the first two months after transformation. Sexual maturity is quickly reached and the frogs participate in the next season's breeding choruses. Hamilton (1934) found that *Bufo terrestris* would double in size during the second growing season, and he felt that they would contribute to the breeding chorus at 2 years of age. Raney and Lachner (1947) found that these toads grew much more slowly as adults, probably reaching a maximum at 3 or 4 years. Blair (1953) found that *Bufo valliceps* would reach the size of sexual maturity, and contribute to the breeding chorus when 10 months old. Jameson (in press) reported that *Syrnophus* will reach the size of sexual maturity in 3 to 4 months, the males will call at 4 months, and the frogs born early in the spring may contribute to the fall breeding population. Ryan found that *Rana pipiens*, *Rana clamitans* and *Rana catesbeiana* will all reach the age of sexual maturity one year after transformation

and that some of these might possibly contribute to the first breeding populations, but that most will require 2 years. Undoubtedly these data are severely affected by the environmental situations. *Hyla* and *Bufo* breed in semi-permanent and permanent rain pools and ponds during rainy seasons. The terrestrial *Syrnophus* breeds during both the spring and fall rainy seasons. The *Rana* on the other hand tend to breed throughout the summer in more permanent situations. Although the inherent characteristics of growth in different species cannot be precisely related, the studies presented to date indicate that anurans have certain factors in common. There is a very rapid increase in size immediately following transformation with a considerable reduction in rate after cooler weather arrives. Some increase is noted during the second year, after which growth continues very slowly.

Dispersal of juvenile treefrogs was found to occur after they had spent several days in protected places near the pond. Moisture from a heavy dew is available almost every evening of the summer in western Oregon. This behavior is in contrast to that of the juveniles of *Bufo valliceps* which remain in aggregates near the pond until stimulated to disperse by a heavy summer rain (Blair, *op. cit.*) The cliff-frogs probably remain in the protection of the moist rocky areas where they are born until conditions are favorable for dispersal, for very small individuals are not found until the nights following summer showers.

Dispersal distances are unknown for juvenile *Rana*. One *Bufo valliceps* moved about 800 yards. Seventeen juvenile *Syrnophus* moved from 123 to 328 yards (mean 231 ± 28) while *Hyla regilla* appeared to disperse less than 200 yards.

The particular pond utilized for the dispersal study had very little nearby vegetation, and the local cover was not nearly as extensive as generally occurs in ponds in the Willamette Valley. This may have resulted in both higher losses and in greater dispersal distances. Tall grasses surround most of the breeding ponds, and the juveniles were commonly found in these grasses throughout the summer and fall. Juveniles were not found immediately to the dispersal pond after the first week in August.

The pond was completely dry the last week in August. The dispersal distances noted in *Hyla* at this locality were not great enough to carry the frogs to other breeding ponds in the area. Undoubtedly many individuals dispersed farther than 200 yards and were not found. In many parts of the Willamette Valley ponds are much closer and some gene flow must occur. The amount of gene flow would depend on the tendency of the frogs to return to the pond where they hatched. Two of the 30 frogs known to survive long enough to find cover away from the pond were recovered in the pond the following year. Adult females were seldom recovered. If we assume an equal survival for both males and females and an equal number of each sex, there were about 15 males of the 30 juveniles which one would expect to recover.

The known information about *Bufo*, *Rana* and *Syrrophus* and the homing studies in *Hyla* indicates that migration of adults is not to be expected except under adverse conditions. Thus most of the gene flow is attributable to juvenile dispersal and this gene flow in *Bufo valliceps* and *Hyla regilla* appears to be rather low. In these species it may be advantageous if most of the individuals do not go outside of the original area, since it is probably more important to maintain a somewhat inbred population of moderate size than dispersed small populations which may be destroyed by predators.

Dispersal of a given number of individuals into populations of low density and small size is proportionally higher than dispersal of an equal number of individuals into populations of high density and large size (Wright, 1943). The actual space occupied by breeding units of the Pacific treefrog may be much smaller than an entire pond because the pond is divided into smaller units by the structure of the breeding population (Jameson, in press). Low dispersal numbers will tend to favor both adaptive and non-adaptive differentiation when population densities are low and population sizes are small as appears to be true in this treefrog.

The high rate of turnover and the low percentage (11 percent) of survival (38 of 373 frogs survived one year at the permanent pond) indicate an intensive loss of individuals. We may estimate that two (13.3 percent) of 15

marked juvenile *Hyla* survived their first year. Hamilton (1934) and Raney and Lachner (1937) indicated that many individuals of *Bufo terrestris* live from 3 to 5 years. Blair (1953) found that 11.2 percent (20 of 178) of the juvenile male *Bufo valliceps* survived the first year. Sixty-six percent of the adult *Syrrophus* disappeared in one year and 81.5 percent were lost in 18 months. Ryan (1953) recorded adult *Rana pipiens* and *Rana catesbeiana* which survived 10 months and adult *Rana clamitans* which survived 17 months. Raney and Ingram (1943) recorded a *Rana catesbeiana* which survived 23 months.

Only 13 of 239 (5.4 percent) of the *Hyla* larger than 33 mm. and only one of 136 frogs larger than 35 mm. were recovered one year later, but 25 of 92 (27.2 percent) smaller than 32 mm. were recovered. It is probable that many of the treefrogs reach 35 mm. in one full year's growth after transformation (Table I). These data could indicate that the larger individuals were more susceptible to predation. If we assume that from any one time (in this case the few weeks of marking) each individual had an equal opportunity for loss of life from predators, then we might assume the larger individuals were dying of old age. However, 4.2 mm. growth was noted in the largest frog recovered after one year. The trauma of marking may be more rigorous for the larger frogs than the smaller but this is very doubtful. The larger frogs appeared to be more active in June and July during the day (when perhaps subject to greater attack by gartersnakes) than the smaller ones. This could indicate more the habits of the observer than that of the frogs. It may be that the smaller frogs left the pond earlier in the summer than the larger, and were perhaps thus not as subject to predation.

Known predators in the ponds studied include the introduced bullfrog (*Rana catesbeiana*), the Pacific gartersnake (*Thamnophis ordinoides*), and the red-sided gartersnake (*Thamnophis sirtalis concinnus*). More than 20 gartersnakes and 17 bullfrogs were removed from the permanent pond in the summer of 1953. These predators obviously took a heavy toll of the frogs and the larvae. The removal of the snakes and bullfrogs from the pond probably accounts for the increase in the number of *Hyla* in

1954 (630 marked in 3 nights) over 1953 (373 marked in 18 nights). A millpond about 50 yards south-east of the dispersal study pond had a large population of bullfrogs (*Rana catesbeiana*) and no adult *Hyla* were heard calling from this pond nor were any *Hyla* egg masses or larvae observed.

It is felt that the bullfrogs had taken all the *Hyla* from the millpond and prevented their return. It was noted in general that in ponds where the bullfrog was common in the Willamette Valley, *Hyla* choruses, egg masses or larvae were never found. This predatory activity by the bullfrog may also account for the absence of native *Rana* in the Willamette Valley in areas where they were once common.

One of the most critical times in the life of an amphibian is immediately following transformation. Considerable metabolic readjustment is made, or not made, at this time in the usual change from a herbivorous to carnivorous (insectivorous) diet. The apparent tendency of the "baby" frogs to "aggregate" near the accustomed habitat of water makes them particularly susceptible to predation. One red-sided gartersnake captured at the dispersal study pond was found to contain 52 juvenile *Hyla*, all right at or just past transformation, each with only a small part of the tail remaining. Apparently on this occasion those that still swam fish-like and those which had completely absorbed the tail were better able to escape. Both of these latter groups were much more numerous than the type taken by this snake. On the other occasions snakes were found with most sizes of both larvae and juveniles in their stomachs.

The very low percentage of survival (2 of 1,156 juveniles and 38 of 373 adult *Hyla*) found in this study is apparently well compensated by the number of eggs laid by each female (500-1,000). The number of adult males in the breeding chorus at the dispersal pond appeared

to be less than 200 in the spring of both 1953 and 1954.

SUMMARY

Growth, dispersal and survival were studied in marked populations of the Pacific treefrog. Thirty juveniles that were marked shortly after transformation were found to approximately double their size in 2 months. The frogs were found to reach breeding size in 8 months and to contribute to the breeding chorus at that time. Sexually mature individuals were found to grow considerably less than juveniles but growth appeared to continue at all sizes. Most juveniles were found to disperse less than 200 yards but some undoubtedly move much farther. Only 11 percent (38 of 373) of adults marked in 1953 were recovered in 1954. This small number of returns indicates a very rapid turnover in the population, probably due to predation. The information obtained in this study is compared with similar studies on *Bufo*, *Syrrophus* and *Rana*.

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Emergence, Breeding, Hibernation, Movements and Transformation of the Bullfrog, *Rana catesbeiana*, in Missouri

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MANY aspects of the life history of the bullfrog (*Rana catesbeiana* Shaw) remain little investigated, despite its importance as a game and laboratory animal, and its widespread distribution in North America. The most comprehensive information on the life history of the species is to be found in writings of Wright (1914, 1920) and Wright and Wright (1949, and earlier editions). A general account was presented by Dickerson (1931). Detailed studies of several phases of the life history of the species in Louisiana were made by George (1940). In New York, Raney (1940) and Ingram and Raney (1943) reported movements of the bullfrog; growth rates were investigated by Raney and Ingram (1941) and Ryan (1953). In Missouri, food habits of the bullfrog have been studied in detail by Korschgen and Moyle (in press). These substantial contributions have been augmented by several brief scientific papers, and by popular accounts originating in various states. Nevertheless, the bullfrog has received considerably less attention from researchers than have game fishes, birds, and mammals of similar importance.

In Missouri, high rank in the commercial production of bullfrogs was achieved many years ago. In 1908, the commercial harvest of frogs was higher in Missouri than in any other state (U. S. Department of Commerce and Labor, 1911). Bullfrogs undoubtedly contributed a large share of this take. After the early 1900's, the bullfrog resource declined, but the recent expansion of habitat resulting from construction of thousands of farm ponds in this state has set the stage for recovery. Bullfrog populations sufficiently large to afford sustained hunting for sport, at least can be hoped for.

This study was undertaken to provide information on the life history and management of the bullfrog in Missouri. The work was begun in February, 1950, and some data were collected as late as April, 1954. During the first 2 years, the work was performed by Moyle, and was confined to farm ponds, most of which

were located in Boone County in central Missouri. These ponds ranged from one-fourth acre to 2 acres in area and had maximum depths of from 6 to 15 feet; many of the ponds were of a type approved for construction subsidies and for fish stocking by federal and state agencies.

In the second two-year period, the study was made by Willis. The 1952 collections were also made in central Missouri farm ponds, but in 1953, some streams in central Missouri, and ponds in the southwestern portion of the state were included.

EMERGENCE AND SONG

Field observations were made on 38 days in the spring of 1950 and on 68 days in the spring of 1951 to determine dates of emergence from hibernation and the commencement of singing. The presence or absence of frogs was recorded and a coarse measure of abundance kept, but actual counts of frogs seen or heard were not made. Air temperatures were obtained from the United States Weather Bureau station at Columbia, Missouri. Surface water temperatures in shallow portions of the ponds were recorded in 1951, but not in 1950.

Bullfrogs were first seen in 1950 on March 23, and in 1951 on March 28. In 1954, two large bullfrogs were observed on a pond bank on February 9, during an unseasonably warm period. However, seasonable temperatures soon returned and in subsequent observations made for about a month, no bullfrogs could be found.

In 1950 and 1951, the years in which systematic observations were made, the very small bullfrogs, evidently those which had metamorphosed the previous year, were seen first. For the next 2 or 3 weeks, increasing numbers of these small frogs were observed. Then, for 1 or 2 weeks, the large bullfrogs were noticed in ever increasing numbers. By May 2, 1950, and April 28, 1951, bullfrogs of all sizes were abundant in most ponds. The earlier emergence of small bullfrogs was much more striking in 1950 than in 1951, so this pattern may not hold

TABLE I
EMERGENCE DATES FOR THE BULLFROG IN VARIOUS
LOCALITIES OF THE UNITED STATES

| Locality | Jan. | Feb. | Mar. | Apr. | May | Reference |
|------------|--------------------------|------|------|------|-----|--------------------|
| New York | ... | ... | ... | ... | X.. | Wright (1920) |
| New York | ... | ... | ... | X.. | ... | Ryan (1953) |
| Ohio | ... | ... | ..X | ... | ... | Walker (1946) |
| Missouri | ... | ... | X.. | ... | ... | This study |
| California | ... | ... | X.. | ... | ... | Pickwell (1947) |
| Texas | ... | ..X | ... | ... | ... | Dawson (1953) |
| Kansas | ... | X.. | ... | ... | ... | Smith (1950) |
| Florida | ... | X.. | ... | ... | ... | Fla. D. Ag. (1952) |
| Gulf Coast | X.. | ... | ... | ... | ... | Viosca (1934) |
| Louisiana | ... | ... | ... | ... | ... | George (1940) |
| | Active throughout winter | | | | | |

in all years. However, early appearance of small bullfrogs near Ithaca, New York, was noted during the same two-year period by Ryan (1953); Pope (1944) also mentioned this phenomenon.

Published dates of emergence for bullfrogs in various localities in the United States together with similar information from this study, reflect, with some exceptions, a northward progression in times of emergence (Table I). The exceptions may be due to the inclusion

by some authors of unusually early, or temporary appearances.

Emergence of bullfrogs is greatly influenced by temperature. Evidences are many: the northward progression of emergence dates, early emergence in unseasonably warm periods, and the winter-long activity (Dickerson, 1931) in large springs, presumably with nearly constant water temperatures.

A relationship existed between air and water temperatures and numbers of bullfrogs which could be found during the present study (Figs. 1 and 2). During 1950 and 1951, first emergence evidently occurred during warm periods, and few bullfrogs could be found during the brief cooler periods which followed.

Wright (1914) wrote that the appearance of bullfrogs could be expected in New York when (maximum) air temperatures reach 68° to 75°F., provided the temperatures at the water-bottoms are at least 57° to 64°. In central Missouri in 1951, bullfrogs emerged when surface water temperatures were about 55°. Maximum air temperatures on the days of emergence in 1950 and 1951 were 66° and 71°, respectively. Thus, agreement with Wright's temperature data is rather close.

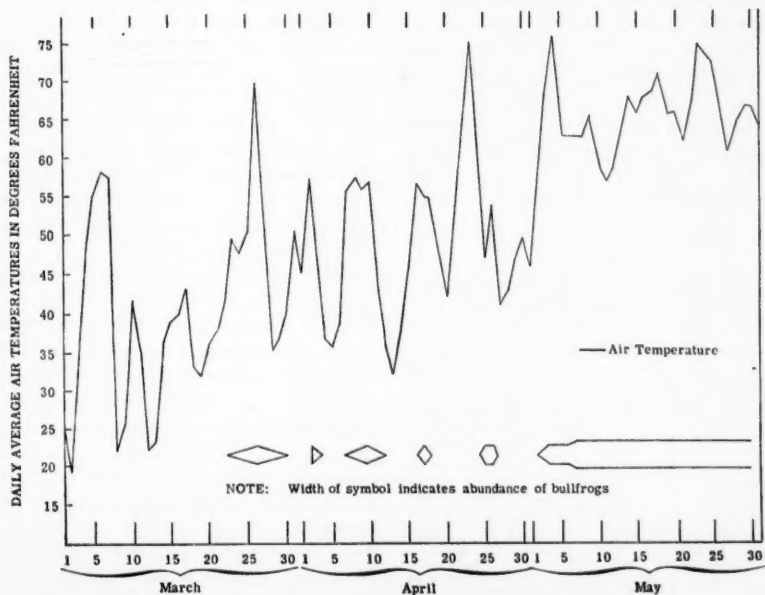


Fig. 1. Abundance of bullfrogs in relation to air temperatures, 1950.

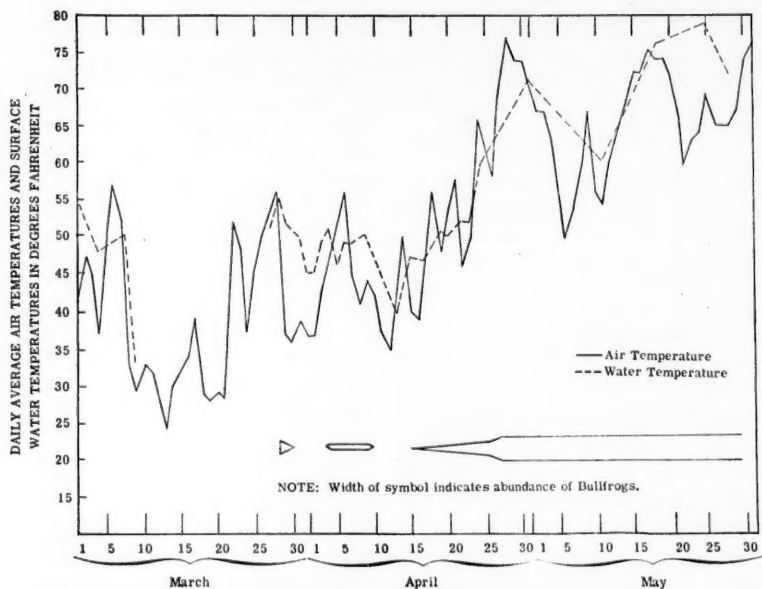


Fig. 2. Abundance of bullfrogs in relation to air and water temperatures, 1951.

Ryan (1953) found small bullfrogs emerging in the vicinity of Ithaca, New York, on April 18, 1950 and April 9, 1951. These dates are much earlier than Wright's records on about May 15 and thereafter for the same area. The maximum air temperature at Ithaca on the day of emergence in 1950 was 70°, well within Wright's range; in 1951, the maximum temperature recorded at the U. S. Weather Bureau at Ithaca was only 56°, but it was 64° on the day previous to emergence.

The first bullfrog song of 1950 was heard on April 8; in 1951, April 25; and in 1954, April 25. Individual song continued, except for short interruptions, until the first chorus was heard on May 13, 1950, and May 17, 1951. Chorusing continued somewhat sporadically, until the period June 14–25, 1950, when extremely loud choruses were heard night and day. In 1951, only sporadic chorusing was heard. In 1950, the chorus diminished after June 25, and ceased by July 8. In 1951, choruses were rarely heard after July 15. In both years, breeding continued after chorusing ceased.

Published records of the time of initiation of song in various localities of the United States, together with information from the present study, also indicate a northward progression (Table II). Since most of the authors did not state when song ceased, it is impossible to determine from the literature the duration of singing in most other localities.

In the present study singing started late enough in the spring that temperatures were generally trending upwards. However, song and chorusing showed no clear relationship to day-to-day changes in air or water temperatures. For example, during the period April

TABLE II

INITIATION OF SONG BY THE BULLFROG IN SEVERAL LOCALITIES OF THE UNITED STATES

| Locality | Feb. | Mar. | Apr. | May | Reference |
|-------------|------|------|------|-----|-------------------------|
| New York | ... | ... | ... | ..X | Wright (1920) |
| U. S. | ... | ... | ... | ..X | Dickerson (1931) |
| East. U. S. | ... | ... | ... | ..X | Morris (1945) |
| Ohio | ... | ... | ... | ..X | Walker (1946) |
| Iowa | ... | ... | ..X | ... | Carlander et al. (1950) |
| Iowa | ... | ... | ..X | ... | Bailey (1944) |
| Missouri | ... | ... | ..X | ... | This study |
| Florida | ... | ... | ..X | ... | Fla. D. Ag. (1952) |
| Texas | ... | ..X | ... | ... | Baker (1942) |
| Gulf Coast | ..X | ... | ... | ... | Viosca (1934) |
| Louisiana | ..X | ... | ... | ... | George (1940) |

25 to 27, 1950, air temperatures were as high as 75°, but no bullfrog song was heard. It is possible that song is controlled by other factors such as gonadal development, being limited only by extremely high or low temperatures.

TIME OF BREEDING

Published statements of the time of breeding of bullfrogs in different regions of North America are evidently based on varied amounts of actual field work. Although methods used in determining the breeding season were not stated by most of the authors, apparently they usually relied upon finding egg masses. In the exceptional case, Wright and Wright (1949) examined the gonads of 35 frogs at Dorset, Ontario, Canada on June 28–29, 1913, and found that none of the females had yet spawned.

The onset of the breeding season (approximate) for bullfrogs in several regions of the United States and Canada is progressively later from south to north. Also, there is a much

greater duration of the spawning season in the south (Table III).

Wright and Wright (1949) attributed the lateness of onset of breeding in New York to the late emergence and short period of activity at that latitude. Conversely, bullfrogs remain active during much of the year in the Gulf States (George, 1940; Florida Depart. of Agri., 1952), and there they could be expected to breed earlier.

Moore (1942) showed a relationship between the relative lateness of the breeding seasons of the common eastern frogs and the lower limits of temperature tolerance of the embryos of those species. He found that the bullfrog has a high minimal temperature for development which is the same at the northern and southern extremes of its range in the United States.

In the present investigation, breeding was studied by analysis of female gonads rather than by observation of egg masses because the latter could not be found in sufficient numbers. Frogs for this analysis were collected during

TABLE III
ONSET, DURATION, AND PEAK OF BREEDING FOR THE BULLFROG IN VARIOUS REGIONS
OF THE UNITED STATES AND CANADA

X = breeding season as stated in reference; x = duration of breeding uncertain

| Locality | Feb. | Mar. | Apr. | May | Jun. | Jly. | Aug. | Sep. | Oct. | Nov. | Reference |
|------------------|------|------|------|------|------|------|------|------|------|------|-------------------------|
| Iowa | ... | ... | ... | ... | ... | XXX | X.. | ... | ... | ... | Carlander et al. (1950) |
| Ontario, Canada | ... | ... | ... | ... | ..X | xxx | ... | ... | ... | ... | Wright et al. (1949) |
| New York | ... | ... | ... | ... | ... | XXX | ... | ... | ... | ... | Raney (1940) |
| New York | ... | ... | ... | ... | ..XX | XX | ... | ... | ... | ... | Wright (1914, 1920) |
| Northeast U. S. | ... | ... | ... | ... | ..XX | XX | ... | ... | ... | ... | Wright et al. (1949) |
| New York | ... | ... | ... | ... | ..XX | X.. | ... | ... | ... | ... | Ingram et al. (1943) |
| "Farther north" | ... | ... | ... | ... | ..XX | Xxx | ... | ... | ... | ... | Viosca (1934) |
| U. S. in general | ... | ... | ... | ... | ..XX | XXx | ... | ... | ... | ... | Cochran (1932) |
| Kansas | ... | ... | ... | ..XX | Xxx | x.. | ... | ... | ... | ... | Smith (1950) |
| California | ... | ... | ..X | XXX | XXX | XXx | ... | ... | ... | ... | Storer (1933) |
| Texas | ... | ... | XXX | XXX | XXx | ... | ... | ... | ... | ... | Baker (1942) |
| Gulf States | ... | ... | ..XX | XXX | XXx | xx | ... | ... | ... | ... | Viosca (1934)* |
| Louisiana | ... | ..X | XXX | Xxx | xxx | x.. | ... | ... | ... | ... | George (1940) |
| Florida | ... | ..X | XXX | XXX | XXX | XXX | XXX | XXX | XXX | X.. | Fla. D. of Ag. (1952) |
| Texas | ..XX | ... | ... | ... | ... | ... | ... | ... | ... | ... | Wright et al. (1949) |

* Also U. S. Fish and Wildlife Serv. (1944).

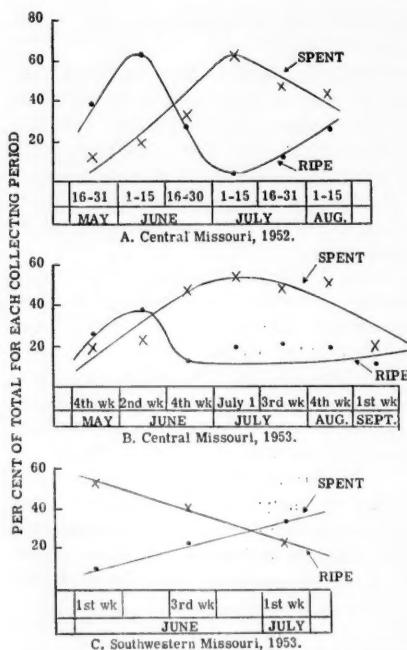


Fig. 3. Percentages of spent and ripe bullfrog ovaries in the 1952 and 1953 collections.

1952 and 1953. In the first year, collecting was confined to farm ponds in Boone and Callaway counties, central Missouri. In 1953, collecting operations were extended to include state-owned warm-water fish hatchery pools in southwestern Missouri, as well as streams and ponds in the central part of the state.

The frogs were killed at the termination of each collecting trip, refrigerated overnight, and gonads were removed the next morning. This procedure allowed the blood to congeal in the vessels; otherwise, the gonads had to be washed individually to remove the fresh blood which stained the eggs in the preserved ovary. Descriptions of color of the gonads were made upon removal, as the color often changed markedly in preserved specimens.

All frogs were dead when measured; a fish-measuring board was used. The left hand was placed flat on the frog's back and considerable pressure applied to straighten out the vertebral column. Body length was considered to be the distance from the tip of the snout to the end of the urostyle; in preliminary trials as many as 15 measurements of one frog fell within a three-millimeter range.

Time of breeding was established by comparing the percentages of females with gonads in the different developmental stages at various dates. It was found that few frogs smaller than 128 mm. (5.0 inches) in body length had spawned; it was also found that some larger than 128 mm. had immature ovaries. Therefore, only gonads from individuals of 128 mm. or greater in body length, and in developmental stages other than immature, were used in analysis of breeding (Table V).

To facilitate analysis and presentation of the data, each female gonad was assigned to one of five stages of breeding readiness (Tables IV and V; Fig. 3). Since several frogs already had spent ovaries by the second half of May, some breeding may have occurred earlier than

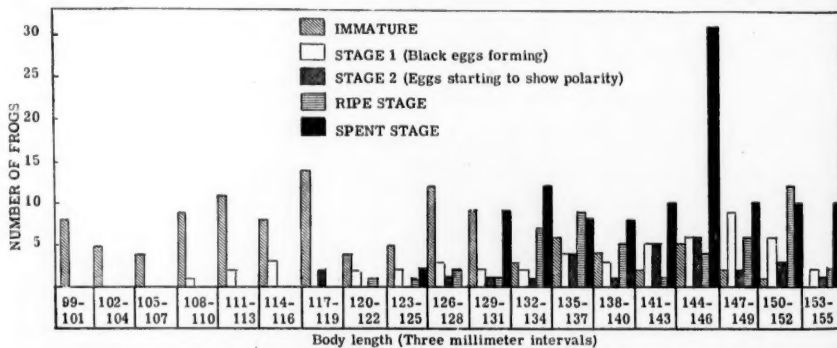


Fig. 4. Stages of breeding readiness of ovaries of 350 bullfrogs.

TABLE IV

FIVE STAGES OF BREEDING READINESS IN THE REPRODUCTIVE CYCLE OF THE BULLFROG

Sizes of eggs and oviducts are general approximations and probably apply to no more than 80 percent of the material assigned to each stage

| Stage of breeding readiness | Oviduct characteristics | Ovary characteristics |
|-----------------------------|--|--|
| | | |
| Immature | Very small; colorless; translucent; size in cross section: up to 1×2 mm. | Ovary yellow; no black pigmentation on eggs; most transparent, others opaque and yellow-cream to light brown. Egg size: up to 0.5 mm. in diameter. |
| #1 | Small; opaque; light cream to light orange colored; size in cross section: 2.3×3.3 mm. | Ovary black; black eggs predominant, although some eggs not so advanced are gray or brown; also a few may show polarity. Egg size: up to 0.75 mm. in diameter. |
| #2 | Same as stage #1, often slightly larger; size in cross section: 2.5×3.8 mm. | Polarized eggs predominant; most vegetal hemispheres dark or light gray, some white or brown. Egg size: up to 1.0 mm. in diameter. |
| Ripe | Colorless; translucent; much enlarged; easily broken or damaged. Size in cross section: 3.0×6.0 mm. | Ovary much enlarged; polarized eggs predominant; most vegetal hemispheres white, a few gray or brown. Egg size: up to 1.0-1.6 mm. in diameter. |
| Spent | (a) Normally small; opaque; cream to orange in color. (b) As in ripe stage in very freshly spent ovaries; size in section: 1.0×3.0 mm. | Ovary flaccid; shrunk; pale yellow; devoid of black eggs (except occasionally a few unshed, mature eggs are present) some developing eggs may be brown in color. |

that; bullfrogs began emerging in the middle of April in central Missouri.

In general, the data for both years indicate that there was much breeding activity during June and early July, as evidenced by the decrease in percentages of ripe ovaries and the increase in percentages of spent ovaries in collections taken during and between these dates.

TABLE V

THE DEVELOPMENT OF FEMALE BULLFROG GONADS TAKEN IN CENTRAL AND SOUTHWESTERN MISSOURI IN 1952 AND 1953

| Collecting period | Number of frogs | Percentage of frogs in various stages of breeding readiness | | | |
|--------------------------|-----------------|---|-------|------|-------|
| | | No. 1 | No. 2 | Ripe | Spent |
| 1952 (Central) | | | | | |
| May 16-31 | 8 | 25 | 25 | 38 | 12 |
| June 1-15 | 21 | 9 | 9 | 62 | 19 |
| June 16-30 | 62 | 20 | 20 | 25 | 33 |
| July 1-15 | 26 | 27 | 7 | 4 | 61 |
| July 16-31 | 49 | 20 | 20 | 12 | 47 |
| Aug. 1-15 | 52 | 19 | 15 | 25 | 42 |
| 1953 (Central) | | | | | |
| May, 4th wk. | 16 | 43 | 13 | 25 | 18 |
| June, 2nd wk. | 39 | 23 | 18 | 36 | 23 |
| June, 4th wk. | 15 | 27 | 13 | 13 | 47 |
| July 1 | 69 | 13 | 14 | 19 | 54 |
| July, 3rd wk. | 15 | 20 | 13 | 20 | 47 |
| Aug., 4th wk. | 14 | 14 | 14 | 21 | 50 |
| Sept., 1st wk. | 26 | 46 | 24 | 12 | 19 |
| 1953 (Southwest.) | | | | | |
| June, 1st wk. | 39 | 20 | 15 | 54 | 10 |
| June, 3rd wk. | 35 | 14 | 23 | 40 | 23 |
| July, 1st wk. | 18 | 11 | 33 | 22 | 33 |

Both in 1952 and 1953, in central Missouri, the frogs having the highest percentage of spent ovaries were collected in early July (Fig. 3). The percentages of spent gonads decreased in subsequent collections, some probably being identified as redeveloping stages. Thus, the peak of breeding must have occurred during early July, or before. The fact that there was a sharp decline in percentages of ripe ovaries during the latter half of June, and only a low percentage of frogs (1952, 25 percent; 1953, 13 percent) remained in breeding condition by the last week of that month, suggests that the peak of breeding occurred about the last week of June in both years. The southwestern Missouri data are too few to be conclusive, but there, too, late June is indicated as the peak of breeding.

Each breeding female bullfrog may lay 10,000 to 20,000 eggs (Wright, 1920). Neither the extent of mortality nor the stage in the life cycle at which mortality is heaviest is

known. But in the absence of such knowledge, it seems possible that relatively few successful breeders might be necessary to replace adult losses in the population. In the present study about half the mature females had spent ovaries by July 1, 1952. Fifty-four percent of 67 females taken on July 1, 1953, had spent ovaries. These facts, coupled with the possibility that relatively few breeders are needed, indicate that the July 1 opening date for bullfrog hunting in Missouri is a satisfactory one.

The duration of the spent condition is not known; therefore, it is not possible to calculate what proportion of the spent ovaries in late July and thereafter (Fig. 3) is due to breeding after mid-July and what percentages result from breeding previous to that time. However, some late breeding is known to occur, as an egg mass was found in a central Missouri farm pond on August 28, 1953. Little breeding is thought to have occurred in September or later, and most of the frogs with spent ovaries taken during this period had probably spawned earlier.

SIZE AT SEXUAL MATURITY

The literature reveals that considerable disagreement exists concerning minimum body size of mature bullfrogs, the lengths reported varying from 85 to 127 mm. Some of this variation may be due to regional differences, but some of it doubtless reflects the fact that different criteria for maturity have been used by different authors.

Wright (1932) examined the bullfrogs in the collections of Cornell University and the United States National Museum and concluded that they became sexually mature at 85 mm. Wright and Wright (1949) gave 89 mm. as the minimum length for adult females, but remarked that the species seldom breeds until it reaches 100 mm. The interpretation of minimum adult length was actually based on external characteristics (Wright, *in litt.*).

Raney and Ingram (1941) studied growth rates of tagged bullfrogs in New York and concluded that the average individual reaches 85 to 105 mm. in body length and sexual maturity 2 years from the time of transformation; slow-growing frogs might not breed until 4 years after transformation. However, these

workers apparently judged sexual maturity by the ease with which females could be recognized as such rather than by their actual ability to breed.

The stages of breeding readiness of ovaries from 350 bullfrogs collected during this study were arranged according to body length (Fig. 4). The smallest females with spent ovaries fell in the 123–125-mm. body-length group (4.8–4.9 inches). This must approach the minimum breeding length for females under Missouri conditions, for only one frog of lesser body length was found to have ripe ovaries. These findings agree closely with those of George (1940) who stated that some female bullfrogs became sexually mature at 127 mm.

Many females larger than 123–125 mm. had immature ovaries. But the sex of several of these was easily recognized by secondary characteristics; thus, it seems doubtful that breeding abilities can be positively diagnosed by external characteristics alone.

HIBERNATION

Field observations relating to hibernation were made in 1950 and 1951, in two farm ponds located near Columbia, Missouri. During both years, large bullfrogs seemed to react to cooler fall nights in two ways. During the moderately cool nights of September, they became increasingly wary, often jumping into the water even before the observer could approach within 40 feet. As nights became cooler, the large frogs deserted the pond banks and floated at the water's surface. This behavior almost always occurred when the air was cold and the surface water temperature was higher than the air temperature. Such floating was first observed on October 5, 1950 and during later periods when daily average air temperatures fell below about 60°–65°. When warm spells intervened with average air temperatures of 65°–70° and over, and with the air again warmer than the water, large bullfrogs were once more seen on the banks around the ponds.

After the floating habit had been noted for about 3 weeks, a gradual decrease in the number of large frogs began. Hibernation of some bullfrogs must have begun by October 23 when this decrease in numbers was very evident and when air and water temperatures fell below 60°. On October 24, when the air temperature

at the ponds was 42° and the surface water temperature was 57°, only a very few large frogs were seen, and these were floating. Seining the pond bottoms produced torpid bullfrogs of the same size class. A short interlude of warmer weather brought renewed activity of frogs, but on November 9, freezing temperatures occurred for the first time. By November 14, no large frogs remained active. Similar observations in 1951 showed that hibernation of some large individuals commenced about October 20; bullfrogs remained scarce, and after October 31, no more were seen.

In New York, Raney and Ingram (1941) observed that most of the bullfrogs seemed to have gone into hibernation by the last of September. Wright's (1914) latest autumnal record for Ithaca, New York was October 14, 1899, but Ryan (1953) collected active, small bullfrogs as late as November 10, 1949, at Ithaca.

The pre-hibernation behavior of Missouri bullfrogs is apparently somewhat similar to their mid-winter behavior in Florida, where "From the first cold days of winter till the first warm days of February, they are rarely seen . . . However . . . during prolonged periods of warm weather they may be observed in mid-winter, disappearing again as the weather turns cold." (Florida Depart. of Agri., 1952). Similarly, George (1940) reported that at Baton Rouge, Louisiana, bullfrogs are more or less active in all seasons, disappearing during cold spells, but reappearing in shallow water during warm periods.

In the Missouri study, small bullfrogs were seen in abundance until freezing temperatures prevailed. There was no evidence of the pre-hibernation behavior seen in the adults and they were found on pond banks and in shallow water. During this period, the small bullfrogs may be susceptible to heavy mortality from sudden, hard freezes. Differential mortality of the small bullfrogs during the autumn-to-spring period was suggested by tagging studies. Of 32 bullfrogs about 75 mm. in length, tagged in the fall of 1950, only one (3 percent) was recaptured during 1951. But of 89 frogs 100 mm. or larger, tagged at the same time and place, 43 (48 percent) were recovered in 1951. Although egress may explain the failure to recapture the small

bullfrogs, this seems somewhat unlikely, for a group of ponds was under observation.

MOBILITY

Detailed studies of the movements of tagged bullfrogs and greenfrogs (*Rana clamitans*) were reported in New York by Raney (1940) and Ingram and Raney (1943). Returns from 237 tagged bullfrogs showed that movements of individuals within a single season varied greatly; some moved as little as 10 feet, but one moved 4,000 feet. The greatest total movement was 5,250 feet by one frog, tagged in 1939 and recaptured in 1940. Raney (1940) concluded that movements did not appear to correlate with spawning, food-getting, temperature changes, or other tangible factors.

A strong homing tendency in a pet bullfrog was reported by McAtee (1921) and homing of a few individuals was also noted by Raney (1940) and Ingram and Raney (1943). In the work of Raney (1940) a group of bullfrogs was released in a pond 240 feet distant from the pond of capture. Nineteen were recaptured, but only two of these returned to the original pond; thus, there was little evidence of well developed homing behavior.

In the present study, bullfrogs were marked for recognition by applying numbered fingerling fish tags to the upper jaws. All tagged frogs were released in the ponds in which they were captured. Movements within ponds were studied on two half-acre ponds located near Columbia, Missouri. Both ponds were covered in detail and numbered stakes were placed every 20 feet along the shore line. Observations were made by wading the ponds at night, recapturing frogs, and recording the locations on maps.

One hundred and fifteen usable records of intra-pond movements were obtained from 31 of the 72 individuals tagged in the two ponds during the period June–September, 1951. Forty-one frogs either were not seen after release or else were seen only during June. The latter records were discarded, owing to the short time spans involved.

To analyze intra-pond movements of the 31 individuals, shore line distances between the most widely separated points of recapture of each individual were measured and compared with the total length of shore line. Of the 31

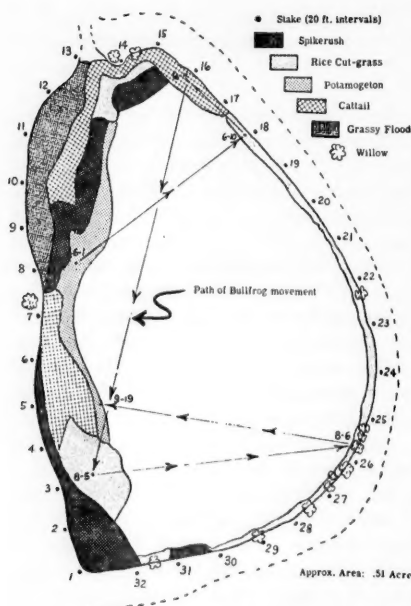


Fig. 5. Extensive bullfrog movement without pattern.

frogs, 26 (84 percent) utilized more than one-eighth (90 and 80 feet, respectively) of the total shore line of the two ponds, while only five frogs (16 percent) used one-eighth or less. Of the 26 frogs utilizing more than one-eighth of the total shore line, 23 exhibited a type of movement in which no definite pattern or cover type preference was discernible (Fig. 5). Three of the 26 frogs exhibiting extensive movements frequently returned to a small section of the shore line (Fig. 6).

In this study, as contrasted with the work of Wright and Wright (1949), the occupancy of individual perches during the croaking season by male bullfrogs was not noted. In fact, it was impossible to draw conclusions on any aspects of territoriality among bullfrogs due to lack of observation of daily activities of the species. The fact that so many of the frogs utilized a large proportion of shore line seems to argue against their being territorial. However, it may be that in ponds so small, territories overlap considerably.

For the study of movement between water areas, bullfrogs in three large groups of ponds

were tagged; a total of 17 ponds was used. Within each group the ponds were so arranged that some frogs could move as little as one-tenth of a mile or as much as one mile in traveling from one to another. No pond was more than a half-mile from the nearest one of its group. One group of seven ponds was checked about once a week while the others were visited at bi-weekly or greater intervals.

Of 264 tagged frogs in the 17 ponds, 21 (8 percent) were known to have moved from one pond to another during the period June, 1951 to July, 1952. Assuming straight-line movements, the distances traveled between ponds were as follows: 0.6 mile, one frog; 0.5 mile, two frogs; 0.4 mile, 15 frogs; 0.25 mile, mile, two frogs; and 0.1 mile, one frog.

The longest total overland movement was at least 0.75 mile, and was made by a frog which moved from one pond to another and then returned to the first. The first part of this journey was made in early July, and probably involved traveling at least 0.25 mile across a bare field which had recently been harrowed. Another frog, tagged on May 20, 1951, was recovered on July 10, 1952, at a pond 0.4 mile distant from

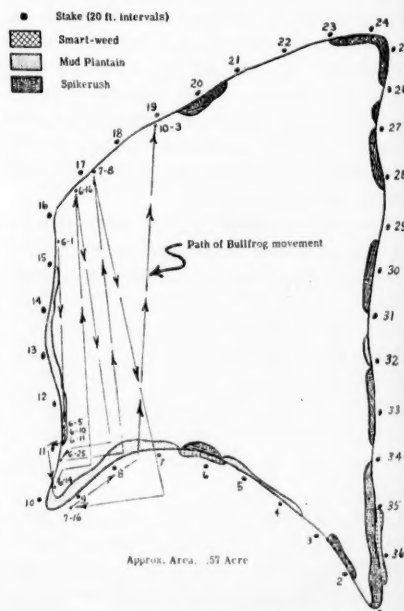


Fig. 6. Extensive movement of one frog.

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the tagging point. In covering this distance, the frog had to cross a gravel road bordered by two brushy fencerows, two fields, and it probably crossed a densely vegetated gully.

Since only 8 percent of the frogs tagged in this study were known to move from one pond to another, it seems that the spread to new water areas must either be brought about by the movements of a very few individuals or must be accomplished mostly by ingress of frogs smaller than 50 mm., the minimum length of those tagged. Sometimes, however, the spread into new impoundments is rapid (Klimstra, 1949; Rosene, 1951). That very small bullfrogs might be important in such rapid stocking of new waters was indicated by the following observations in this study. During the first week of July, 1951, at least 20 newly metamorphosed bullfrogs arrived in a recently filled pond. During this period, frogs of the same size were found in temporary pools, and were seen hopping along the roads at night. It is possible that, of the large frogs often found in one- or two-year-old impoundments, many did not enter as adults, but moved in soon after transforming and then were able to grow very rapidly because of the abundant food. This possibility was strengthened by the collection from a two-year-old pond of six female bullfrogs well above the minimum size for breeding (about 125 mm.) but all with immature ovaries.

GROWTH AND TRANSFORMATION OF TADPOLES

The age of bullfrog tadpoles at transformation varies considerably in the United States, with the following extreme ages reported: 4 months in Louisiana (George, 1940), and 3 years in New York (Wright, 1920). The age at transformation is progressively greater to the north (Table VI).

In Missouri, growth and transformation of tadpoles were investigated during two seasons by stocking bullfrog tadpoles (1951) and eggs (1952) in a small pond which had been enclosed with a four-foot fence made of one-quarter-inch mesh hardware cloth. Both years before stocking the pond was drained, all amphibians removed, and the pond refilled.

In July, 1951, about 700 bullfrog larvae, collected as eggs several days previously, were placed in the enclosure. One hundred and seventy-six of them were measured 3 months

TABLE VI
AGE OF BULLFROG TADPOLES AT TRANSFORMATION
IN VARIOUS PARTS OF THE UNITED STATES

| Locality | Number of winters of life before transformation | | | | Reference |
|-------------|---|---|---|---|-------------------------|
| | 0 | 1 | 2 | 3 | |
| New York | . | . | X | X | Wright (1914) |
| Iowa | . | . | X | X | Carlander et al. (1950) |
| California | . | . | X | . | Storer (1922) |
| Iowa | . | X | . | . | Klimstra (1949) |
| Florida | . | X | . | . | Fla. D. Ag. (1952) |
| Louisiana | X | ? | . | . | George (1940) |
| Gulf States | X | X | . | . | Viosca (1934) |

later, in September. At this time they averaged 35 mm. in body length (from tip of snout to junction of under side of body with tail).

A bullfrog egg mass was stocked within the enclosure on July 1, 1952, and produced tadpoles with body lengths of 24–38 mm. (av. 29.6) and total lengths of 70–102 mm. (av. 86.1), by May 3, 1953. Although this period totalled 10 months, probably not more than 4 to 5 months of growth were involved.

Similar rates of growth for tadpoles in Louisiana were found by George (1940), who stocked an enclosure with an egg mass on April 27 and measured the tadpoles 4 months later, on August 29. At that time, their average body length was 32 mm. and average total length was 84 mm.

Within the Missouri enclosure, young bullfrogs in late transformation stages were found on June 1, 1953, 11 months (one winter) after the eggs were placed in the pond. Klimstra (1949) in Iowa, is the only other worker who positively reported such a short larval life at central United States latitudes. However, George (1940) found transformation starting in his enclosure in Louisiana about August 26, only 4 months after eggs were stocked. Most of his tadpoles had transformed by September 7. He concluded that tadpoles, varying in size, transform approximately at the same time and produce frogs proportional in size to the tadpoles.

In Missouri, the earliest date on which transforming tadpoles were observed was June 1, 1953; they were seen as late as early October. The greatest numbers of transforming frogs were observed in late June, July, and early August.

SUMMARY

This study of phases of the life history of the bullfrog in Missouri was made during the period February, 1950 to April, 1954. Most, but not all, of the data were collected in the central part of the state.

Systematic observations were made during 1950 and 1951 to determine dates of emergence. Very small bullfrogs were found first, with the large frogs following in number a few weeks later. Adult bullfrogs appeared exceptionally early during a warm period on February 9, 1954, but this early appearance was only temporary.

Emergence of bullfrogs is greatly influenced by temperature. Air and water temperatures in Missouri at the times of emergence agree rather closely with those given for New York state by other authors.

The first bullfrog song of 1950 was heard on April 8; in 1951 and 1954 singing was not heard until April 25. Chorusing, first heard on May 13, 1950, and May 17, 1951, virtually ceased by mid-July; some breeding continued after its cessation.

Time of breeding was determined by analyses of ovaries. Breeding began by mid-May; several females collected during that period in both years had spent ovaries.

In central Missouri during 1952 and 1953, and in southwestern Missouri during 1953, the breeding peak apparently occurred in late June. It is thus indicated that the July 1 opening date for bullfrog hunting in Missouri is a satisfactory one.

The duration of breeding is not known, but one bullfrog egg mass was found as late as August 28, 1953.

The smallest females with spent ovaries fell in the 123-125-mm. body-length group (4.8-4.9 inches), and this must approach the minimum breeding length for female bullfrogs under Missouri conditions.

Large bullfrogs began hibernating earlier than small ones. Active frogs were no longer seen after mid-November, 1950, and the last of October, 1951.

Movements of bullfrogs within two half-acre ponds were studied by recapturing tagged frogs. Of 31 frogs yielding usable records of movement, 26 used more than an eighth of the shoreline of the ponds (80-90 feet). No definite

pattern of movement within these ponds was discernible for most of the frogs.

Of 264 bullfrogs tagged in 17 ponds located in clusters, 21 (8 percent) were known to have moved from one pond to another during the period June, 1951 to July, 1952. The longest total overland movement was at least 0.75 mile.

Observations indicated that the ingress of newly transformed bullfrogs may be an important factor in the stocking of new ponds.

Data were presented on the growth rates of bullfrog tadpoles. It was shown that these tadpoles can transform after one winter, under Missouri conditions.

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Comparative Features of the Life Histories of *Ambystoma gracile* (Baird) from Populations at Low and High Altitudes

RICHARD C. SNYDER

THE life cycle of *Ambystoma gracile* is one of considerable variability, the details of which are incompletely known. Watney (1941: 16) stated that in the vicinity of Vancouver, British Columbia, the eggs are deposited in March, April and May and that the larvae show marked differences in metamorphic behavior. Some of the larvae transformed during the first year, others did not metamorphose until the second spring, while still others remained in the water as paedogenic forms for an unknown length of time. While Watney based her conclusion of paedogenesis on a 125-mm. gravid larva and upon longevity records of 2½ and 4 years for captive larvae, Slater (1936: 234) has furnished the sole description of egg deposition by a larval animal. In Pierce County, Washington, depending upon season and altitude, egg deposi-

tion (by adults) may occur from January to mid-July (Slater, 1936: 235). Carl (1943: 28) indicated that at sea level in British Columbia eggs are laid in February, March, April and May and that larvae spend at least one year in the water, some transforming in the second summer when 2½ to 3½ inches in length while others remain as larvae for indefinite periods and, in some cases, breed. These latter larvae may be found in ponds from sea level to timberline and often attain a length of 5½ to 6 inches.

Carl and Cowan (1945: 43) remarked upon the puzzling diversity of size and color pattern at metamorphosis in British Columbia. At sea level, the majority of larvae transform at the age of 12 to 14 months and the adults are uniformly brown or black with no evidence of spotting. Larvae taken from altitudes of 2,100

to 3,600 feet did not metamorphose until they were fed beef thyroid after a period of 2 to 4 years in captivity; the adults from these locations were dark brown, spotted with black dorsally and marbled with yellow on the sides and venter. Storer (1925: 76) recorded a series of larvae taken in 1911 from Mt. Rainier National Park, Washington. These animals were of various sizes and in various stages of transformation; the largest was 160 mm. in length while the smallest metamorphosing larva was 108 mm. Logier (1932: 316) described an additional series of 23 larvae collected near Vancouver, British Columbia at 3,500 feet that ranged from 52 to 157 mm. in length, and first pointed out the possibility of the retention of larval characters in montane populations to a considerably larger size. Previously, Slevin (1928: 27) reported that larvae nearly ready to transform were taken in cold mountain streams at 8,000 feet on Mt. Rainier, Washington. Although I have not seen these specimens, it is probable that they represent neotenic individuals for reasons to be set forth below. Henry and Twitty (1940: 249) described the presence of many large *A. gracile* larvae in Frog Heaven pond at an altitude of 4,400 feet on Mt. Rainier, stating that they were of such a size as to have soon reached metamorphosis or "which might have functioned as axolotls." Bishop (1943: 130) obtained both adults and larvae from the same pond. Recently, Farner and Kezer (1953: 454) collected large neotenic individuals from and in the vicinity of Crater Lake National Park, Oregon, at altitudes between 4,000 and 5,300 feet. A population in Spruce Lake was composed of "large neotenic individuals, smaller larvae of several size classes, metamorphosing larvae and completely metamorphosed individuals."

The above review indicates that neoteny, or a tendency toward it, is a normal characteristic of *A. gracile* populations and that neotenic individuals coexist with larvae destined to metamorphose at both low and high altitudes. As Watney (1941: 16) has pointed out, the factors responsible for the failure of certain individuals of this species to metamorphose are unknown. It is the purpose of this paper to present additional observations which will add to our knowledge of the life cycle and some of its variable features, particularly with regard

to metamorphic behavior of larvae, the effect of altitude on neoteny, and larval¹ breeding. Concomitantly, several other features of the life history are described.

Field and laboratory studies have been carried out intermittently over a three-year period (1952 through 1954). Adults, larvae and eggs have been collected from ponds in the vicinity of Seattle and from higher elevations in Mt. Rainier National Park. The most intensive collections have been made from the following localities: (1) a pond on the farm of Lewis Weiss, six miles southeast of Woodinville, Washington; (2) a pond along Route 5A, three miles east of Kent, Washington (both ponds approximately at sea level); (3) Tipsoo Lake (5,500 feet), Frog Heaven ponds (4,500 feet), and Ricksecker Point pond (4,300 feet), all glacial cirque ponds on Mt. Rainier.

Larvae taken from ponds and those raised from eggs in the laboratory have been maintained in 30-gallon aquaria for periods up to 2 years under identical conditions of food, light and temperature. The aquaria were supplied with slowly running tap water. Very young animals were fed on enchytraed worms while older larvae received earthworms and liver. Larvae from low and high altitudes, and of the first-, second- and third-year age groups, have been observed under conditions of spontaneous and thyroxin induced metamorphosis. Age groups were based upon known size and age of laboratory reared larvae up to a two-year period. A series of 18 one-year-old larvae averaged 44.2 mm. snout-vent length; 14 two-year-old larvae averaged 73.3 mm. There is no accurate method of determining the age of fully grown, wild larvae. That they actually may be of considerable age is indicated by longevity records of adult *A. tigrinum* of 7 and 9 years, a report of 25 years for an albino larva of the same species (Blanchard, 1932: 99), and records of 21 and 25 years for adult *A. maculatum* (Pope, 1937). The maximum recorded age of *A. gracile* (larva) is 4 years (Watney, 1941).

Conventional body measurements have been taken of a series of larvae and adults from both

¹ The term "larva" refers to a sexually mature or immature individual possessing external gills, caudal fin, and other typical larval features; "adult" refers to a sexually mature, transformed salamander; "subadult" refers to a sexually immature, transformed individual.

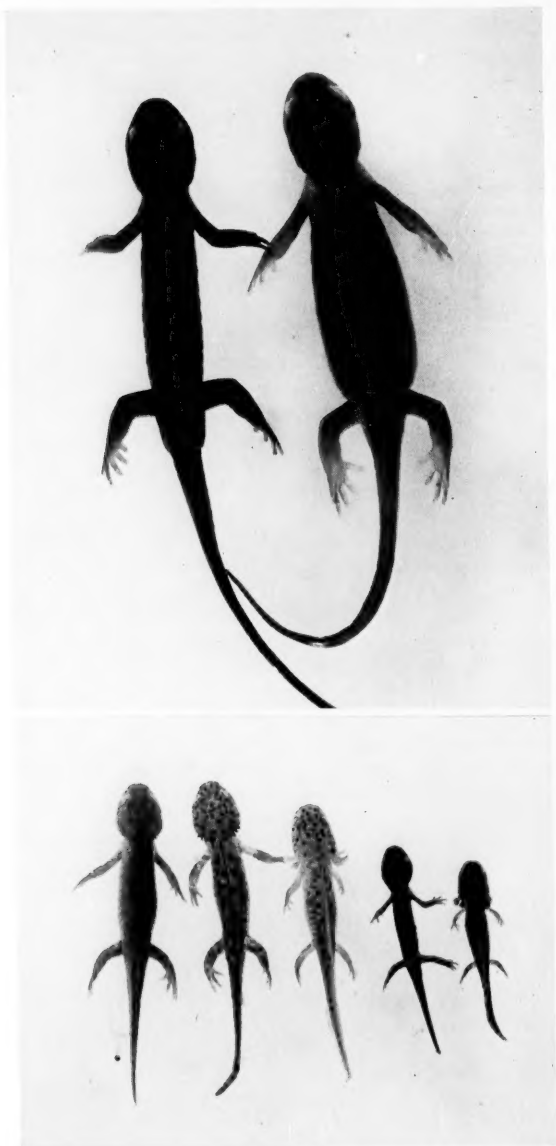
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Upper: Male (left) and female (right) *A. gracile* prior to breeding. Note the darker coloration and the dorsally visible cloacal swelling of the male.

Lower: The three largest animals represent metamorphic stages of a 1-year-old larva (center); the two small larvae on the right show a 5-month larva (far right) and an almost completely transformed subadult of the same age. Reduced one-third.

types of environment and body proportions calculated; these measurements were taken from specimens fixed in 1:16 formalin and stored in 70 percent alcohol. Finally, the salient features of sexual dimorphism and dichromism of larvae have been studied and described. The collections of salamanders upon which all observations are based are housed in the Department of Zoology, University of Washington.

LIFE HISTORY AT SEA LEVEL

In the vicinity of Seattle, the adult salamanders emerge from hibernation and move to the breeding ponds in late January or early February; the peak of emergence occurs during the latter part of February although individuals continue to arrive at the ponds until the middle of March. The initial appearance coincides with a mean air temperature of between 40° and 45° F. and is accompanied or preceded by rainfall. At this time, the salamanders may be found concealed in the leaf litter bordering the ponds, usually in direct contact with water. Collecting at approximately weekly intervals following the appearance of the first animals resulted in the following numbers of males and females: 2-0, 5-0, 6-0, 16-3, 8-2, 0-1, 1-2. While these figures may represent an actual higher proportion of males, it is also possible that they reflect a difference in habits. It is not known whether males actually precede females to the ponds and there are indications that the majority of females enter the water directly upon arrival and do not linger on the borders. In spite of diligent searching in 1953 and 1954, only three females were taken along the edges of the Rt. 5 pond; the first indication of the presence of numerous females was the appearance of eggs in the pond.

There are no striking sexual differences except during the breeding season. At this time, males tend to become darker in color and the greatly enlarged cloacal lips are conspicuous (Pl. I). The legs of the male, particularly the hindlimbs, are slightly longer and larger than those of the female.

The first egg masses are found in the ponds during the last week of February, a time coincident with the middle of the emergence period. Egg laying continues for a period of 6 to 7 weeks, the climax of deposition occurring

during the fifth and sixth weeks, judging from the relative numbers of freshly deposited masses found in the ponds. Such egg masses can be identified not only by the cleavage status of the individual eggs, but also by the small size of the jelly mass which takes a period of 3 to 4 days to enlarge to its maximum size. The eggs are almost invariably attached to sticks, plant stems, or other objects in the water. The appearance of the eggs and the mode of attachment have been described by Slater (1936: 235), Bishop (1943: 130), Stebbins (1951: 34) and others.

Although the breeding behavior of this species has not been witnessed, the extended periods of emergence, migration to water and egg laying indicate that the breeding period begins slowly and gradually builds to a climax, the duration of reproductive activity averaging about 5½ weeks in any one pond.

The reproductive tracts of 13 males, selected at random from groups collected between February 5 and March 20 in 3 consecutive years, were characterized by maximally enlarged testes and the presence of quantities of spermatozoa in the ductus deferens. Microscopic examination of the testes showed very few spermatozoa and no evidence of active maturation; most of the cells in the tubules were spermatogonia. All of these animals were collected in the leaf litter near the water. Two additional males, collected February 15 in a pile of half-rotted logs about 70 feet from the pond, had not yet emerged from hibernation. The testes of these salamanders were enlarged and showed several clumps of mature spermatozoa; most of the tubules were empty, however, and the epididymis was packed with spermatozoa. The ductuli deferenti contained only a few sperm cells. Although additional evidence is needed, it appears that the evacuation of spermatozoa from the testes is complete or nearly complete by the time spring emergence from hibernation begins and that male salamanders may not enter the water until the ductus deferens is filled. The events of 1953 offer corroborating evidence. The month of January was marked by unusually heavy rainfall (12.92 inches) and a mean monthly temperature of 44.3° F, higher than in February (40.2°). Male salamanders appeared on February 1, twenty days earlier

than in either 1952 or 1954. The first indication of egg laying was six fresh masses noted on February 21. Since these eggs had been deposited the previous day, 19 days had elapsed between the first appearance of males and actual breeding. That this interim period was probably not due to the absence of females is indicated by the collection of two females containing mature ova on February 6.

Unsuccessful attempts were made to collect post-breeding adults for the purpose of gonadal examination. Several adult males were therefore maintained in laboratory terraria for varying periods of time and the testes examined at intervals following the breeding period. Those examined in July showed many spermatocytes, spermatids and a few mature spermatozoa; very few spermatogonia were present. In September and October, the testes contained an abundance of mature and maturing sperm cells and a relative increase in numbers of spermatogonia. Although the salamanders were kept under artificial conditions, it seems reasonable to assume that spermatogenesis begins in late June and July, continues throughout the summer to attain maximum activity in early fall, and decreases during the winter.

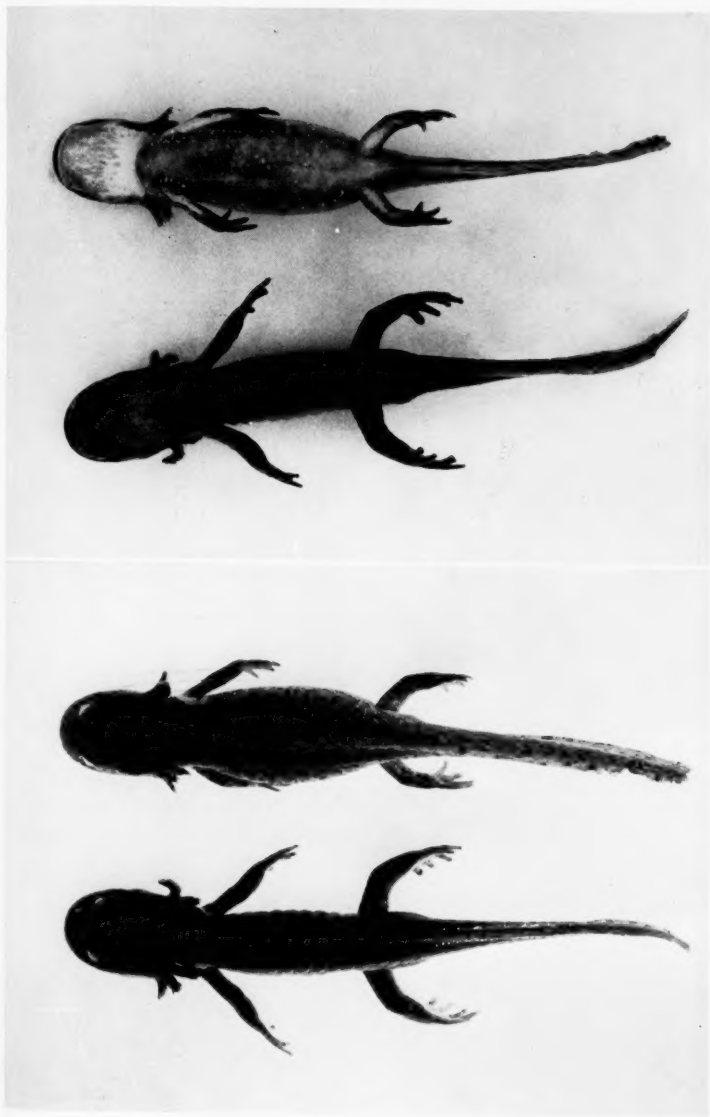
Brief descriptions of the larvae of *A. gracile* were given by Bishop (1943: 132) and Stebbins (1951: 34). The embryo and early (40-mm.) larva was illustrated by Henry and Twitty (1940: 248); Stebbins (1951: 447) pictured a 63-mm. individual. In the vicinity of Vancouver, British Columbia, the larvae stay in the water until the second spring and some of them then metamorphose when they have attained a total length of 75 to 92 mm. and are approximately 1 year old (Watney, 1941: 14). In general, the same situation obtains in larvae of this age and size group collected from several ponds near Seattle. A total of 20 larvae raised in the laboratory, from eggs collected March 16, 1952, transformed from March 7 to 13, 1953. The average size of these animals at metamorphosis was 87 mm. total length. Of 65 year-old larvae collected March 18, 1953, 59 (90 percent) subsequently metamorphosed in the laboratory during March, April and May of the same year. It should also be noted here that of another series of 10 young larvae, raised from eggs in the laboratory and kept in small (10-gal.) aquaria, eight meta-

morphosed at ages between 4 and 6 months at a mean length of 46 mm. (Pl. I). It is doubtful that such early transformation occurs under natural conditions although it is impossible to be sure. Subadults of this size have not been collected, and larvae of comparable size do not show the gill reduction indicative of beginning transformation.

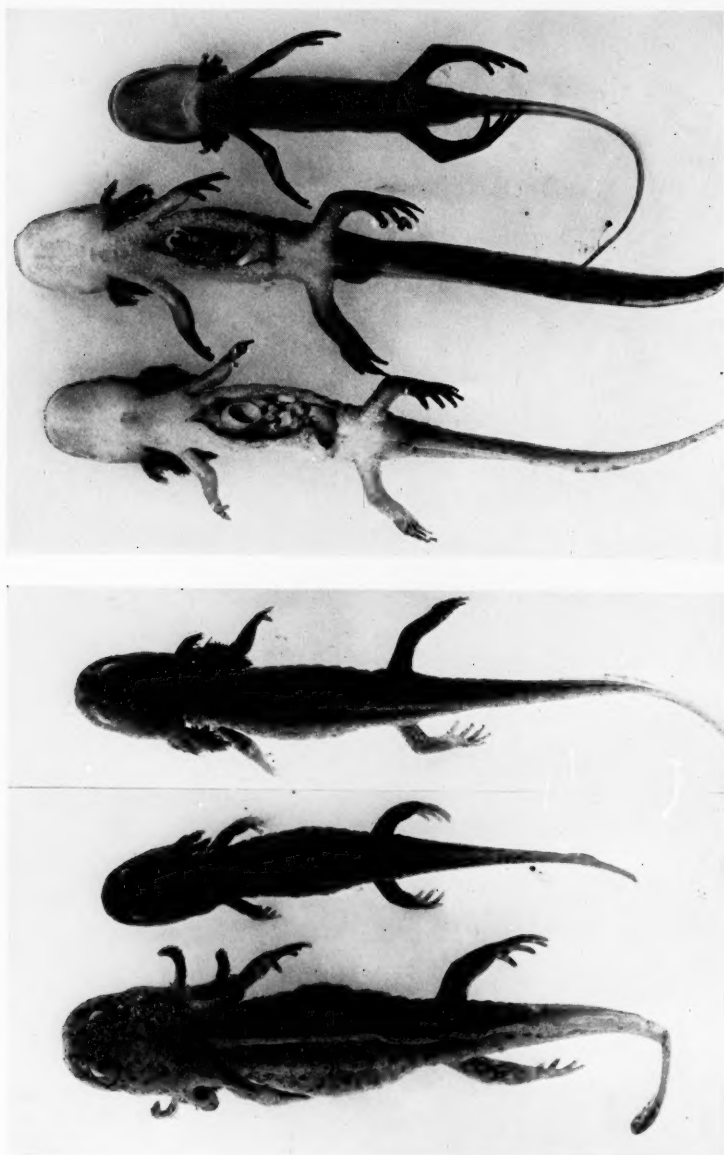
The proportion of larvae that normally undergo metamorphosis to those that remain neotenuous in any one population is not known. Several authors have mentioned neoteny in this species (Watney, 1941; Carl, 1943; Farner and Kezer, 1953) but there is only one reference to paedogenesis (Slater, 1936) and the eggs have not been described.

Abundant evidence of neoteny and paedogenesis was furnished through the cooperation of Lewis Weiss who partially drained a 1½-acre pond located on his farm near Woodinville, Washington. This pond is spring fed and overflows into a stream tributary to Sammamish Slough through a system of narrow ditches passing through drained marshland. Previous to this operation on March 17, 1953, Mr. Weiss had removed 50 gallons of amphibian egg masses (*A. gracile* and *Rana aurora*), all that he could find. A search for salamanders made in the drainage ditches on March 18 and 19 yielded 240 larvae along with numerous masses of freshly deposited eggs. No adult salamanders were found with the exception of a few *Taricha granulosa*. On November 7, 1953, the pond was almost completely drained for the second time and 113 additional larvae were collected. Since many larvae were missed either in the soft mud bottom of the pond or in inaccessible pockets of the drainage ditches, the larval population may be conservatively estimated at around 400 individuals. Of the 353 larvae collected, 150 were in the one-year age group, 193 in the two-year age group and 10 in the three+ age group.

The egg masses deposited by the larvae varied from small clusters of 15 to 34 eggs, to large masses containing up to 143. A few bunches were attached to grass stems, but most lay free on the bottom. Without exception, the jelly mass was of a loose tenuous consistency, not firm as in the case in adult egg masses, and there was a pronounced tendency for individual eggs and the surround-



Dorsal (left) and ventral (right) views of male and female (*A. gracile*) pre-breeding larvae from Weiss pond. The darker coloration, lack of spotting, swollen cloaca and hypertrophied limbs of the male are conspicuous. Reduced one-third.



Left: Female larvae of *A. gracile*. From left to right, old (3+ yrs.) individual from Weiss pond; 2-yr.-old larva from Weiss pond; and Tipsoo Lake larva. Right: Tipsoo Lake larvae. From left to right, pre-breeding female; pre-breeding male; and pre-breeding male after maintenance in the laboratory for one year. See text for further explanation. Reduced one-third.

ing jelly coat to protrude from the mass. Most of these clusters were further characterized by peripheral areas of clear jelly which did not contain eggs. Although the waters of the ditch were considerably warmer than that of the pond (and may have been the stimulus for egg laying), the softness of the jelly was probably not due to warm water. While Henry and Twitty (1940: 249) stated that tepid water may have in part been responsible for the softness of egg masses found by them in Frog Heaven pond, larval egg masses collected from this pond shortly after it had become ice-free (water temperature 38° F) were characterized by soft jelly as were eggs collected from Tipsoo Lake in cold water (45°) and eggs deposited in cold, running water in the laboratory. It appears that softness of the jelly mass and the protrusion of individual eggs from it are characteristic features of eggs laid by larvae. In all observed cases, larval eggs have been fertile and the majority have developed normally.

Examination of the larval reproductive organs has shown that sexual maturity is attained during the second year when the animal reaches a snout-vent length of approximately 70 mm. The smallest paedogenic larva in my collection is 60 mm. snout-vent length, the largest 113 mm. The gonads of younger larvae (snout-vent length up to 50 mm.) are very small and show no evidence of gametogenesis, a statement which is also applicable to subadults.

During the breeding season, the degree of sexual dimorphism and dichromism exhibited by larvae is greater than that shown by adults (Pl. II). Males are characterized by prominent swelling of the cloacal lips, hypertrophy of the hindlimbs and feet and well developed paratoid glands. The glandular ridge on the dorsal edge of the tail, described by Stebbins (1951: 33; 1954: 36), is enlarged. The dorsum is dark brown, occasionally with poorly defined darker spots; the venter is almost uniformly dark, flecked with minute, whitish spots. The series of light, lateral line spots (described by Watney, 1941: 15) consists of a single row, low on the sides, with one or two dots to each costal fold. The gular region is uniformly dark brown or black.

The cloacal lips of breeding females are also swollen, although not to the degree noted in males. There is no indication of enlarged hindlimbs or feet and the paratoid glands are less well developed. The dorsum and tail are heavily spotted with dark brown and black and the venter is lighter with larger whitish spots that tend to concentrate laterally. There is either one series of lateral line spots (as above), or, most often, a double series, the upper row occurring high on the sides and occasionally diverging cranially into two rows. The gular region is white or cream colored, heavily streaked with brown anteriorly and tending to become immaculate in the region of the gular fold. Very large females (Pl. III), assumed to be at least three years old, are characterized by considerably less dorsal spotting, obliteration of the upper series of lateral line spots and a darker venter and gular region.

The above differences are apparent not only in the breeding ponds, but also in captive larvae. Under the laboratory conditions, sexual differences became evident early in March. The swollen cloaca and the darker color served to separate pre-ovulatory females from non-breeding females, immature females and immature males. In the pre-ovulatory condition, the ovaries are filled with mature eggs and the oviducts are hypertrophied and heavily vascularized; together, these organs occupy the greater part of the pleuroperitoneal cavity. The reproductive organs of pre-breeding male larvae are similar to those previously described for the adult.

Attempts to induce spermatophore deposition and breeding in the laboratory met with no success. Implantation of 1-3 pituitary glands of *Rana pipiens* or *A. gracile* had no effect, nor did the salamanders respond to the stimulus of warm water after being refrigerated for varying lengths of time with and without pituitary implantation. The administration of extract of mammalian anterior hypophysis, following the method used by Buyse and Burns (1931: 80) for ovulation in *A. tigrinum*, produced no effect although injections were continued for a two-week period. All attempts to induce ovulation and spermatophore production were made at the beginning of and during the normal breeding season.

LIFE HISTORY AT HIGH ALTITUDES

The *A. gracile* populations of the glacial cirque ponds of Mt. Rainier at altitudes above 4,000 feet exhibit interesting diversities. In many such ponds, the bulk of the population consists of large, neotenic larvae, although numbers of smaller larvae of the one- and two-year age groups are represented. In Tipsoo Lake, however, the population is composed of very large larvae; intensive seining of the lake has not revealed smaller animals, nor have any been observed in spite of excellent conditions of visibility. In a total of 16 collecting trips to various ponds and lakes on Mt. Rainier (Tipsoo, Frog Heaven, Ricksecker Point, Reflection and Louise) only three adult salamanders of this species have been seen in spite of diligent searching. One of these was discovered dead in the snow surrounding Tipsoo on July 23, 1953, another was collected from the waters of this lake on August 2, 1953, and the third was collected from Frog Heaven pond on July 17, 1954. Although Bishop (1943: 130) mentioned the finding of adults in the latter pond in 1936, he did not state the number collected.

The scarcity of adult salamanders in or around these mountain lakes is also indicated

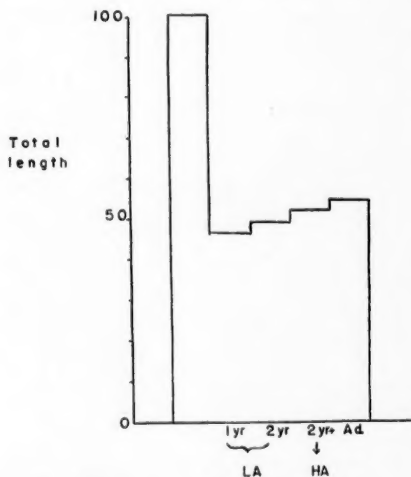


Fig. 1. Effect of age on tail length of *Ambystoma gracile*. LA, low altitude larvae; HA, high altitude larvae; Ad, adults. Tail length is shown as a percentage of total length.

by the small numbers of adult egg masses found during the breeding season. The majority of egg masses found in Ricksecker Point pond, Frog Heaven pond and Reflection Lake are typically larval and only larval eggs have been taken from Tipsoo Lake.

Comparison of larvae from low and high altitudes reveals that the latter are characterized by a generally lighter coloration, indistinct mottling of the dorsum with very little or no spotting, and a greater total length (Pl. III). The increase in length is, however, largely a function of tail length (Fig. 1), a fact which lends support to the probability that the neotenic larvae of mountain lakes live to a considerable age. It has been established by many investigators that the tail forms a greater proportion of the total length in larger and older individuals, a phenomenon recently reported for *Eurycea* (Duellman and Wood, 1954: 96). There is also a tendency toward an increase in hindlimb length in montane larvae, but it is of borderline significance.

During the breeding season, sexual dimorphism of mountain larvae is marked with regard to the cloacal lip swellings and the hypertrophy of hindlimbs and feet. There is considerable variation, however, in color. Males tend to become darker than females dorsally and ventrally, but they never approach the dark brown or black of males from low elevations and the venter is usually mottled (Pl. III). Occasionally, large males have been noted with a uniformly cream colored venter which is similar to that of some breeding females (Pl. III); other females take on the ventral coloration typical of low altitude larvae (Pl. II). Differences in lateral line spotting between males and females are similar to those described above for larvae living at low elevations. However, a complete absence of lateral line spots is characteristic of large (and presumably old) montane larvae (Table I). In discussing the validity of separating *A. gracile* into northern (*decorticatum*) and southern (*gracile*) subspecies, Dunn (1944: 130) remarked upon the absence of these spots in southern larvae and their presence in the northern group. It is evident that this spotting varies with age and sex in larvae collected in the vicinity of Seattle, well below the

TABLE I
SECONDARY SEXUAL CHARACTERS OF BREEDING LARVAL *Ambystoma gracile*

| Dimorphism | | | | | Dichromism | | | |
|----------------------------|--------|------------------|------------------------|-------|-----------------------------|--|---|------------------------------------|
| Altitude: Sea level | | | | | Sea level | | | |
| N | Sex | Cloacal swelling | Costal grooves overlap | Feet | Dorsum | Venter | Gular | Lateral line spotting |
| 10 | Male | Prominent | 4-6 | Large | Plain or faintly spotted | Very dark; white flecks | Uniform dark | 1 series |
| 14 | Female | Slight | 1-4 | Small | Heavily spotted or blotched | Lighter; spotted and blotched | Anterior streaks; uniform white posterior | 1-2 series; none in older larvae |
| Altitude: 4,000-5,500 feet | | | | | 4,000-5,500 feet | | | |
| 17 | Male | Prominent | 5-7 | Large | Plain | Light; plain or blotched | Light; faintly spotted | None (90%); or faint single series |
| 13 | Female | Slight | 2-4 | Small | Reticulate; snout spotted | Uniform light or blotched; a few like sea level larvae | Uniform light | None (90%); or faint single series |

northern limit of distribution of Dunn's southern race.

When larvae from mountain lakes are kept in the laboratory for a period of several months under the same conditions of food, light and temperature as larvae from ponds at low elevations, they gradually assume a darker coloration. In early March, both groups of larvae assume almost identical breeding colors. Montane males do not become quite so dark as low altitude males and are marked by a whitish band across the gular region (Pl. III). The generally lighter coloration of larvae living at high altitudes may be due to a number of factors, such as the type of food, the mineral content of the water and the amount of light during ontogeny (Noble, 1931: 151). No studies have been made of these features.

In each pond examined on Mt. Rainier, with the exception of Tipsoo Lake, breeding takes place as soon as most of the surface becomes ice-free. At altitudes around 4,500 feet, egg deposition occurs in late June or early

July. In 1954, heavy winter snows followed by a cool spring delayed breeding until July 15. For reasons not well understood, the breeding of Tipsoo Lake larvae (5,500 feet) in 1953 occurred about one month after the pond had become free of ice. This lake was almost ice-free on August 2; the first and only eggs were collected on August 29 and the appearance of the eggs indicated that they had been laid 4 to 5 days previously. In 1954, eleven male and nine female larvae were collected at random from this lake on September 2. The lake had only recently become free of ice. Gross examination of the reproductive tracts of seven females showed the presence in five of small, but maturing ova and enlarged oviducts; the remaining two showed no evidence of maturation and the oviducts were not enlarged. The testes of all males were enlarged to about one-half maximum size and the ductuli deferenti had not begun to hypertrophy. Larvae of both sexes were of maximum size, averaging 80.3 mm. snout-vent length. Since pre-breeding

larvae taken from ponds at lower altitudes at corresponding times (recently ice-free) show either maximally enlarged testes or mature ovarian eggs, these findings suggest a marked effect of elevation and low temperatures on gametogenesis and breeding time.

METAMORPHIC BEHAVIOR

As previously noted, the majority of laboratory raised larvae metamorphosed at one year of age. In every instance, these larvae had been raised from eggs collected at low elevations. Some larvae maintained in 10-gallon aquaria metamorphosed at ages between 4 and 6 months, but there is no evidence that transformation ever occurs at this age in natural populations. Larvae of this size group collected from ponds show no indications of beginning metamorphosis, nor do they transform in large aquaria until they attain an age of one year and a snout-vent length of about 40 mm. Conversely, larvae which have attained a snout-vent length of 40 mm. or more often transform into subadults when removed from the pond and maintained in aquaria. Of 65 larvae collected from Weiss pond, 59 (90 percent) metamorphosed within a two-month period (Table II). The remaining six animals had all transformed by the middle of July after a total elapsed time of about 4 months. With regard to larvae in the two-year age group, 88 of 96 salamanders (91.6 percent) eventually metamorphosed after an elapsed time of 18 months in the laboratory; the remaining eight larvae have given no indication of metamorphosis and are, at this writing, 3½ years old. Unlike the behavior of the one-year class, there was no tendency in this group toward the transformation of large numbers of individuals within a relatively short time al-

though the conditions under which both groups were kept were identical. Finally, seven very large larvae, averaging 105 mm. snout-vent length and assumed to be at least 3 years old, showed no metamorphic tendencies over a 3-month period (Table II). It was not possible to follow these animals for a longer time since they were used for other work; one, however, was kept without change for 6 months.

Since the larval populations of the glacial ponds on Mt. Rainier are small, no attempts have been made to assemble large collections. Over a three-year period, 37 large neotenic larvae collected from Tipsoo Lake have been brought to the laboratory and maintained for varying lengths of time (2 to 4 months) without exhibiting any metamorphic behavior. Ten of these larvae were kept in aquaria for 13 months and one animal transformed after 5 weeks of captivity. Several additional larvae from Frog Heaven ponds and Reflection Lake have similarly failed to show signs of transformation in the laboratory. Although the numbers involved are small, the evidence is suggestive. When the scarcity of adults found at high elevations and the results of thyroxin induced metamorphosis are considered, it appears that transformation is uncommon in montane populations.

A total of 18 larvae was used in an experiment designed to test sensitivity to thyroxin and ability to metamorphose. Six of these were mature larvae from Tipsoo Lake, six were mature larvae from Weiss Pond of comparable size to the Tipsoo animals, and six were year-old larvae, also from Weiss Pond. Each of these groups was subdivided into units of two, placed in battery jars and maintained for several weeks, with appropriate controls, in temperatures of 34°, 48° and 70° F. The water in the battery jars contained a 1:500,000 solution of Squibb crystalline thyroxin prepared after the method used by Kezer (1952: 236) and was changed at two-day intervals. The larvae were placed in this solution on April 22, 1953 and examined daily for evidence of metamorphosis (Table III).

None of the larvae transformed over a period of 2 months at the coldest temperature. When removed from the thyroxin solution and placed in tap water at room temperatures ($\pm 70^\circ$), the Weiss Pond larvae metamorphosed while the

TABLE II
SPONTANEOUS METAMORPHOSIS OF
Ambystoma gracile

| Altitude | Sea level | | | | 4000-5500 feet | |
|------------------------|-----------|-------|-------|-------|----------------|---------|
| Age | 4-6 mo. | 1 yr. | 2 yr. | 3 yr. | 1 yr. | 2-3 yr. |
| No. larvae | 10 | 65 | 96 | 7 | 4 | 37 |
| No. transforming | 8 | 59* | 88 | 0 | 1 | 1 |
| Percent | 80 | 90* | 91 | 0 | 25 | 3 |

* Within a two-month period. All had transformed after four months.

Tipsoo larvae did not. The response to thyroxin at warmer temperatures, which approximated the pond temperatures in which the salamanders were found, was more instructive. At 48°, all larvae responded to thyroxin; the Weiss Pond animals showed gill reduction 7 days earlier than did the Tipsoo larvae and completed their metamorphosis, while the latter died after transformation had proceeded about halfway. Whereas both the one- and two-year-old Weiss Pond larvae began metamorphosis at the same time, its completion was attained 6 days earlier by the younger animals. At room temperatures, all larvae responded to thyroxin at about the same time and completed metamorphosis in 9 to 12 days; the yearling larvae completed transformation a day earlier than did the Tipsoo larvae, which, in turn, were two days in advance of the two-year Weiss Pond animals. Control animals gave no indications of metamorphosis.

While it is recognized that the numbers of larvae used in this experiment were not sufficient to justify more than tentative conclusions, it is felt that the results lend support to the hypothesis of a high proportion of metamorphic failure in larvae living at high altitudes, a well known feature of other montane urodeles (Noble, 1931: 295). That cold either inhibits the release of thyroxin or the ability of tissues to respond to its presence is well established, as is the tendency of younger larvae to respond more readily than older animals to the metamorphic effects of thyroxin. In this case, the response of young and mature *A. gracile* larvae became manifest at the same time although the former completed metamorphosis more rapidly. Although a study of age and growth at different temperatures of this species has yet to be made, it is evident that at high elevations the activity and growth period is markedly shorter, averaging about 3 months, than at lower elevations, where, depending on the season, larvae may be active and feeding throughout the year. Sasaki and Nakamura (1937) showed that feeding, growth and metamorphosis were retarded at low temperatures in montane *Hynobius lichenatus* and that neotenic individuals attained an unusually large size, a phenomenon also noted in *A. tigrinum* by Uhlenhuth (1919a: 525; 1919b: 480). It is reasonable to assume that not only do montane

TABLE III
METAMORPHOSIS OF *A. gracile* IN 1:500,000
THYROXIN

| Larval age (yrs.) | N | Altitude (feet) | Temp. (°F.) | Days to change | Meta-morph. complete (days) | Duration meta-morph. (days) | Duration meta-morph. in room temp. (days) |
|-------------------|---|-----------------|-------------|----------------|-----------------------------|-----------------------------|---|
| 2+ | 2 | 5,500 | 34 | .. | .. | .. | .. |
| 2 | 2 | 200 | 34 | .. | .. | .. | 7 |
| 1 | 2 | 200 | 34 | .. | .. | .. | 13 |
| 2+ | 2 | 5,500 | 48 | 32 | Died | .. | .. |
| 2 | 2 | 200 | 48 | 25 | 69 | 34 | .. |
| 1 | 2 | 200 | 48 | 25 | 63 | 28 | .. |
| 2+ | 2 | 5,500 | 70 | 8 | 18 | 10 | .. |
| 2 | 2 | 200 | 70 | 6 | 18 | 12 | .. |
| 1 | 2 | 200 | 70 | 8 | 17 | 9 | .. |

A. gracile grow more slowly, but that they also attain metamorphic size at a later age. The majority are possibly prevented from transforming either by inhibition of thyroxin release, by the failure of tissues to react to thyroxin at progressively later ages, or by the failure of other associated endocrine mechanisms (Allen, 1929; Noble, 1931). The differences in both spontaneous and induced metamorphic behavior between young and old larvae tend to support this statement although the results are not conclusive. The possibility of an inherited defect of the releasing mechanism for thyroxin, known to be responsible for metamorphic failure in certain subspecies of *A. tigrinum* (Noble, 1931: 295), seems unlikely.

As previously indicated, there is no question of metamorphic retardation in an unknown percentage of larvae living at sea level to which the above discussion does not apply. Several factors may be responsible for the failure of larvae to transform after one year. It is possible that larvae from eggs laid in the late period of the long breeding season are prevented, by cooling of the water and a lowered food supply in the fall, from attaining metamorphic size in one year and are forced to pass the second winter as larvae. The majority of this group probably transforms in the second spring or summer. Occasional breakdown of the mechanism for metamorphosis would explain the occurrence of a small number of unusually

large individuals, which, with increasing age, would tend to lose sensitivity to thyroxin and fail to transform. Individuals that attain an age of 2 years as larvae are fully capable of paedogenesis and may breed before transformation occurs. While it is realized that this is one of several possible interpretations which await further study, it is in part supported by what is known of the life history.

SUMMARY AND ACKNOWLEDGMENTS

The early events of the breeding period of *Ambystoma gracile* living at sea level are described. The length of the breeding period is about 5½ weeks.

A high percentage of larvae transform into subadults at one year of age; most of the remainder transform at 2 years of age. A small number evidently do not transform and remain as neotenic larvae.

Neoteny and paedogenesis are described together with the appearance of the egg masses deposited by larvae. Sexual maturity is attained by larvae during the second year. The secondary sexual characteristics are described.

Features of the larval life history at high elevations are compared with those at sea level. Metamorphosis appears to be uncommon in montane populations. Observations on spontaneous and thyroxin-induced metamorphosis are presented and possible interpretations of metamorphic failure at both low and high altitudes are discussed.

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Herpetological Notes

THE RELATIONSHIP BETWEEN THE RINGNECK SNAKES *DIADOPHIS REGALIS* AND *D. PUNCTATUS*.—In the course of an ecological study of the herpetofauna of the Guadalupe Mountains of northern Culberson County, Texas, and Eddy County, New Mexico, difficulty was encountered in identifying some snakes of the genus *Diadophis*. This difficulty led the writer to review the relationship between *Diadophis punctatus* and *Diadophis regalis* in Trans-Pecos Texas, and it became evident that there is little or no basis for separating these two forms as distinct species. The supposed separation of characters appears to have been an artifact of inadequate collecting in the zone of transition.

Four specimens have been examined from the Guadalupe Mountains. One was collected by the writer near White City. There is an example in the Texas Natural History Collection from Carlsbad Caverns National Park, and the Carlsbad Caverns collection contains two specimens. An example which I have not seen is in the Houston Natural History Museum, and was collected by W. F. Pyburn in McKittrick Canyon. Presumably this last individual is the one which Brown (1950, Baylor Univ. Studies) listed as *Diadophis regalis regalis* from the same locality. Because these specimens are of particular interest, I have included a brief review of the characters of the four examined. In three of the specimens the neck band is virtually absent, being interrupted at the angle of the jaw. In the fourth example the band extends only to the fourth scale row, and is broadly interrupted dorsally. In all of the specimens the belly color extends onto the first row of dorsal scales on the most anterior part of the body, but only very slightly. The largest individual, a female, has 181 ventrals, 47 caudals, dorsals 16-17-15, lower labials 7-8. The next largest specimen, another female, has 181 ventrals, 46 caudals, dorsals 17-17-16, lower labials 8-7. The other two specimens are males. One has 164 ventrals, 50 caudals, lower labials 7-7. The other has 163 ventrals, 47 caudals, and lower labials 8-7; in both the dorsals are 15-15-15. In all four specimens the temporals are 1-1, the preoculars and postoculars 2-2, and upper labials 7-7. Total lengths and tail lengths are 360, 57; 344, 57; 265, 50, and 179, 32 mm.

Diadophis punctatus is widely distributed in eastern North America, and extends into western Texas; *Diadophis regalis* is strictly western in distribution. The two forms are allopatric on the basis of known records, but their ranges practically touch just west of the Pecos River. According to Blanchard (1942, Bull. Chicago Acad. Sci. 7 (1)) *Diadophis*

regalis is distinguished from *Diadophis punctatus* primarily on the basis of a high ventral count (204 or more in the specimens examined) and large size. In addition the light ventral coloration usually extends onto the first row of dorsal scales in *regalis*.

Diadophis regalis is thought to consist of two subspecies; a western race, *Diadophis regalis laetus*, in southeastern Arizona and northern Mexico, and a more easterly race, *Diadophis regalis regalis*, in Trans-Pecos Texas, southern New Mexico, north-eastern Arizona, Utah and Wyoming. *D. r. regalis* differs most strikingly from *D. r. laetus* in the absence or great reduction of the neck ring. According to Schmidt and Smith (1944, Zool. Ser. Field Mus. Nat. Hist. 29 (5)), who base their conclusions on Chisos Mountain material, the eastern subspecies is also distinguished by a smaller size and lower ventral count. (Schmidt and Smith believe that the name *regalis* should apply to the more western subspecies, and proposed the name *blanchardi* for the eastern race of *regalis*. Type and paratypes are from the Chisos Mountains. Though possibly justified, this change seems somewhat premature in view of our present knowledge.)

Two races of *Diadophis punctatus* are of concern to us here. *Diadophis punctatus docilis* is the most westerly race of the species, and is known primarily on the basis of a series of specimens from Tom Green County, Texas. *Diadophis punctatus arnyi* occurs just to the east of *docilis* in central Texas, and had a wide range in the Great Plains region. *D. p. docilis* was diagnosed by Blanchard (*op. cit.*) as being generally similar to *arnyi*, but of larger size, and with a higher number of ventrals. Blanchard also stated that *docilis* shows tendencies toward more western members of the genus in body proportions. The neck ring is not interrupted in known specimens of *docilis*, although it is occasionally interrupted in the better known *arnyi*.

If we ignore the species boundaries, these "racial" characters seem to suggest a continuous, uninterrupted clinal increase in both size and ventral count from east to west through *arnyi*, *docilis*, *regalis*, and *laetus*. To make this more apparent I have assembled ventral and caudal counts (more easily expressed than size) for five series arranged from east to west from central Texas to extreme western Texas (Table I). The Burnet and Blanco County specimens are in the University of Texas Natural History collection, and are referable to *D. p. arnyi*. The Christoval sample is referred by Blanchard to *D. p. docilis*. The Terrell County specimens were identified as *D. p. arnyi* by Milstead, Mecham, and McClintock (1950, Texas Jour. Sci., No. 4), although the ventral count is actually closer to *D. p. docilis*.

TABLE I
VENTRAL AND CAUDAL COUNTS FOR FIVE SAMPLES OF TEXAS *Diadophis*, ARRANGED IN ORDER FROM
WEST TO EAST

| Locality | Males | | | | | Female | | | | |
|---------------------------|---------------|----------|-------|---------|------|---------------|----------|-------|---------|------|
| | No. specimens | Ventrols | | Caudals | | No. specimens | Ventrols | | Caudals | |
| | | Range | Mean | Range | Mean | | Range | Mean | Range | Mean |
| Sierra Vieja Mts. | 2 | 224-227 | 225.5 | 53 | 53.0 | ... | ... | ... | ... | ... |
| Chisos Mts. | 2 | 211-219 | 215.0 | 61-64 | 62.5 | 2 | 224 | 224.0 | 55-59 | 57.0 |
| Terrell Co. | ... | ... | ... | ... | ... | 2 | 197-221 | 209.0 | 56-57 | 56.5 |
| Christoval, Tom Green Co. | 6 | 175-193 | 186.0 | 52-58 | 55.0 | 5 | 191-208 | 200.0 | 41-50 | 47.0 |
| Burnet, Blanco Co. | 2 | 161-167 | 164.0 | 49 | 49.0 | 1 | 181 | 181.0 | 41 | 41.0 |

The Chisos Mountain series was referred by Schmidt and Smith (*op. cit.*) to the eastern race of *Diadophis regalis*, and the same identification was given the Sierra Vieja material by Jameson and Flury (1949, Texas Jour. Sci., No. 2). The neck ring is uniformly present in the first three samples, uniformly absent in the last two. Examination of the table shows that the ventral count increases regularly through all the samples in both males and females. Caudal counts present the same general picture with the exception of a reversal in the Sierra Vieja males.

The Guadalupe Mountains lie to the north of the foregoing samples, and material from that area does not fall into the cline just demonstrated. Nevertheless, the Guadalupe series comes from a critical area lying directly between the known ranges of *Diadophis regalis* and *Diadophis punctatus*, and furnishes additional evidence of the relationship of these two forms. As already pointed out, the neck ring is absent in three of the available specimens, and is broadly interrupted in the fourth. Absence or great reduction of the neck ring has been thought to be diagnostic of eastern *D. regalis*. On the other hand, the ventral count is quite low, and falls within the range of *D. punctatus arnyi*. Identification of this material with either species is therefore impossible unless extra "weight" is assigned to a given character, a procedure for which there is no objective basis. Another bit of evidence for intermediacy between the two species is furnished by a specimen from Ft. Stockton, Texas, identified by Blanchard as *D. regalis*. This individual (U. S. Nat. Mus., No. 5178), the most easterly record for the species, possesses a neck ring one scale wide.

If we disregard artificial species boundaries, and consider instead character geography, the evidence at hand leaves no reason to suppose that *Diadophis regalis* and *Diadophis punctatus* are anything but

elements of a single geographically variable species. Apparently there is a gradual increase in ventral count (and probably size) from east to west in western Texas. This variation pattern is superimposed on the more abrupt loss of the neck ring, which seems to be uniformly absent in most of Trans-Pecos Texas and southern New Mexico. Further, the low ventral counts of the Guadalupe Mountain material indicate a rapid decrease in number of ventrols toward the north in extreme west Texas.

A discussion of subspecies boundaries in *Diadophis* in western Texas is outside the scope of the present paper. The purpose here has been to point out the existence of only one species where two were thought to be present. Suffice it to say that the evidence at hand indicates that the subspecies are largely artificial. This artificiality will undoubtedly become increasingly apparent as new material comes to light. Of the racial "units" herein considered, *Diadophis punctatus docilis* seems to be the least justified. Set up almost solely on the basis of ventral count subject to clinal variation, it serves no practical purpose, and might best be discarded.—JOHN S. MECHAM, Department of Zoology, University of Texas, Austin 12, Texas.

BLOOD CHANGES UNDERLYING THE SEASONAL RESISTANCE OF FROGS TO DISEASE.—The resistance of frogs to disease decreases abruptly in the spring, and the basis of this deterioration is of practical concern.

It seems probable that blood changes must at least partly underlie seasonal variations in resistance. This was examined by observing for one year three highly related items: the hemoglobin percentage, the red blood cell count, and the packed red cell volume.

Rana pipiens was used. Because of differences

TABLE I
SEASONAL CHANGES IN HEMOGLOBIN, RED CELLS, AND PACKED CELL VOLUME IN FROGS

| Hemoglobin | | | | Red cells | | | P C V | | | | | |
|------------|-------------------|------|--------------------|-------------------|---------|--------------------|-------------------|------|--------|------|--------------------|------|
| Month | Number of females | Mean | Standard deviation | Number of females | Mean | Standard deviation | Number of animals | | Mean | | Standard deviation | |
| | | | | | | | Female | Male | Female | Male | Female | Male |
| Jan. | 30 | 57.6 | 9.3 | 30 | 467,333 | 54,653 | 64 | 73 | 26.7 | 29.6 | 6.2 | 6.8 |
| Feb. | 25 | 56.6 | 7.8 | 25 | 466,000 | 93,200 | 71 | 79 | 26.6 | 31.1 | 6.6 | 6.8 |
| Mar. | 30 | 57.4 | 12.0 | 30 | 470,000 | 56,155 | 61 | 45 | 29.6 | 30.6 | 6.4 | 10.9 |
| April | 38 | 50.7 | 9.1 | 38 | 458,947 | 50,304 | 61 | 76 | 33.1 | 32.6 | 5.9 | 6.3 |
| May | 35 | 49.8 | 8.6 | 35 | 459,143 | 56,687 | 89 | 53 | 24.2 | 27.6 | 8.9 | 5.8 |
| June | 52 | 42.2 | 4.9 | 51 | 486,863 | 60,531 | 63 | 25 | 24.6 | 27.5 | 5.5 | 4.2 |
| July | 40 | 44.8 | 6.4 | 39 | 480,769 | 67,737 | 60 | 63 | 27.0 | 34.0 | 5.3 | 5.1 |
| Aug. | 40 | 46.6 | 8.8 | 36 | 515,833 | 96,504 | 50 | .. | 24.4 | | 6.8 | ... |
| Sept. | 41 | 52.4 | 10.4 | 41 | 527,073 | 75,558 | .. | 40 | | 30.9 | ... | 5.7 |
| Oct. | 39 | 65.9 | 9.7 | 39 | 499,487 | 31,464 | 67 | 10 | 24.5 | 27.1 | 6.0 | 6.1 |
| Nov. | 38 | 61.3 | 9.7 | 38 | 490,000 | 38,315 | 41 | .. | 25.7 | | 5.8 | ... |
| Dec. | 40 | 56.8 | 4.3 | 40 | 495,500 | 36,194 | 71 | 16 | 26.8 | 31.6 | 6.1 | 4.4 |

due to sex and disease (Kaplan, 1951, Trans. Illinois Acad. Sci., 44: 209-15), the data are restricted to grossly healthy females, except where noted.

Hemoglobin was determined with the Sahli hemometer (100 percent equal to 17 g.), the red cell count with the hemacytometer, and the packed cell volume with the Wintrobe hematocrit. Using the *t* test, all differences were stated to be statistically significant at the 1 percent level.

EXPERIMENTAL DATA.—Frogs had a relatively high percentage of hemoglobin from December through March. A significant but non-uniform decrease followed, ending in June. Hemoglobin concentration then rose, at a progressively increasing rate, until October, when it exceeded the winter level by a significant amount. With colder weather, the hemoglobin dropped back to the winter level.

Frogs had uniformly low red cell counts from January through March. The counts then de-

creased, although not significantly, until mid-April, when they rose significantly but unevenly until early September. In the colder months, they returned unevenly to the January level.

Female winter frogs had relatively low packed cell volumes (PCV), which rose to a significantly high level in April. They fell to a minimum in May, after which they returned unevenly to the winter level. The decrease from April to May was especially great in females that had just laid their eggs.

Except for the spawning season, male PCVs were significantly higher than those of females, but the cyclic changes were essentially similar.

DISCUSSION.—Blood changes accompany the varying resistance in both sexes. Halsapfel (1937, Quart. Rev. Biol., 12: 65-84) stated that the changing resistance is inherently cyclic.

The animals have a significant anemia, which progressively worsens throughout the breeding season. Hemoglobin falls even with food being offered and despite the internal fat body reservoir. In the female, hemoglobin precursors may be diverted into the eggs.

With the initial rise in hemoglobin concentration in June, frogs improve in weight and vigor. Winter

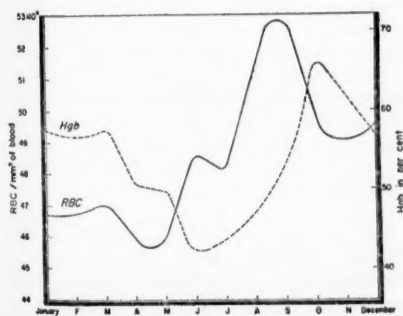


Fig. 1. Seasonal variations in the female frog of hemoglobin and red cells. The dotted lines show variations of hemoglobin (expressed in percentage). The solid curve shows variations in the red cell count; multiply the ordinate values by 10⁶.

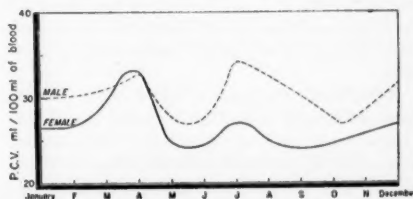


Fig. 2. Seasonal variations in the frog of the packed cell volume. The dotted curve is for the male and the solid curve for the female. The ordinate values are in ml. per 100 ml. of blood.

frogs are not so large, but they too are healthy and vigorous.

When the hemoglobin first falls, the red cells, already relatively low in number, also tend toward further reduction. The bone marrow is reactivated in May, and the red cell count rises. Production of hemoglobin lags about a month behind.

Holmes (1934, *The biology of the frog*: ix + 373 pp.) said that frog blood regenerates in the spring, the marrow becoming lymphoid. The marrow in the autumn becomes fatty and erythropoiesis decreases. Winter frogs maintain a fairly constant output of cells chiefly from the spleen.

In March and April a rising PCV accompanies a falling red cell count. The plasma volume is thus decreasing disproportionately. The blood is concentrated.

In mid-summer the PCV rises with the red cell count, particularly in the male. In view of the plethoric appearance of summer frogs, the findings are interpreted as a rise of plasma volume accompanied by a considerably greater increase in red cells. Hann (1927, *Biol. Generalis*, 3 (1/2): 1-14) found a marked increase in the total plasma volume of frogs in the early summer.

In the late summer and early fall, while the red count is still increasing, the PCV falls. The blood volume is apparently increasing at a greater rate than the red cells.

The statement of Halsapfel (*op. cit.*) that the highest red cell counts occur at or near the breeding season is at variance with the loss of vigor at that period, and is not based on statistical treatment.—HAROLD M. KAPLAN AND GEORGE T. CROUSE, *Department of Physiology, Southern Illinois University, Carbondale, Illinois.*

A LONGEVITY RECORD FOR GILA MONSTER.—Two Gila monsters, at the present writing (April 26, 1955), have been maintained in captivity for over 24 years. They were collected by Theodore Austin in Arizona in September, 1930. The animals were placed in a glass box (25" × 17" × 17") with a screen cover, and kept between two windows in one corner of a laboratory. They now measure 19" and weigh 650.2 g. and 668.6 g., and are quite sluggish. They receive one fresh egg every two weeks and if it is eaten they are given a second egg. Adequate water supply is always present in a dish.

The Gila monsters were a little less than one-half their present size when they were first brought in. It may be safely assumed that they must now be more than 25 years old.—ARTHUR M. CROSMAN, *Biology Department, Washington Square College of Arts and Science, New York University, New York, New York.*

PSEUDACRIS BRACHYPHONA IN TENNESSEE.—The mountain chorusfrog, *Pseudacris brachyphona*, has long been known to occur both to the north and south of Tennessee but locality records of the species within the state are exceedingly scarce, if not absent. On the night of April 23, 1955, while driving northward along U. S. Highway No. 25, several choruses of *P. brachyphona* were heard in Campbell County, between Duff and Jellico. Two specimens were collected from a roadside puddle at Duff. On the night of March 20, 1954, I heard a few choruses of the species along Tennessee Highway No. 28, in Pickett County, between Forbus and Chanute, but no specimens were taken.—ROGER W. BARBOUR, *Department of Zoology, University of Kentucky, Lexington, Kentucky.*

EXTENSION OF THE RANGE OF EUMECES FASCIATUS IN OHIO.—On August 8, 1951, I collected a specimen of *Eumeces fasciatus* Linn. about one mile north-northwest of Castalia, Erie County, Ohio. On this day I had my herpetology class searching for specimens in the pits and pools and under logs and slabs of calcareous tufa in the old abandoned strip-mined area of the Castalia Prairie.

When I came up to an old rotting log bridge across one of the ditches, I saw a skink go skittering along one of the logs until it reached the bank. There it concealed itself under a slab of tufa. I captured the specimen, and in its successful struggle to free itself, it left a wriggling tail in my hand. The animal dived under a pile of tufa and debris. Since further attempts to find the specimen were unsuccessful, the tail was kept as evidence and is now in the collection at the Ohio State University, Franz Theodore Stone Institute of Hydrobiology, Put-in-Bay, Ohio.

Conant (1951, *The reptiles of Ohio*, 2nd Ed.: 28-32, 209-11, 269) reported no collections of this species in Erie County or in any of the adjoining counties. Although the whole specimen was not held long enough to permit a thorough examination, the limited examination before and after capture, the close examination of the tail, and a consideration of the type of habitat and geographical location leave little doubt that this was a specimen of *Eumeces fasciatus*.—N. WILSON BRITT, *Franz Theodore Stone Institute of Hydrobiology, Ohio State University, Put-in-Bay, Ohio.*

DUPLICATE FEEDING HABITS IN SNAKES.—In the summer of 1950 a Davis Mountain ratsnake (*Elaphe subocularis*) was captured near Shafter, Presidio County, Texas. This animal was taken to Austin, Texas, where it was kept alive for approximately 6 months. On September 22 two

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white-ankled, mice *Peromyscus pectoralis* were placed in the snake's cage. The snake immediately grasped one of the mice with its mouth and drew a single constrictor loop about the prey with the anterior one-third of the body. After 3 or 4 minutes the snake released its oral grasp and drew the loop, still constricting the mouse posteriorly, to the middle one-third of the body. This mouse appeared dead. A brief moment later the second mouse ventured close by and the snake, still holding the first mouse, captured and constricted the second. Thus for some 10 minutes the snake was constricting two mice at the same time. After releasing the mice, both were consumed.

In the fall of 1953 two bullsnakes, one a *Pituophis melanoleucus catenifer* from Eugene, Lane County, Oregon, the other a *P. m. deserticola* from near Sunter, Harney County, Oregon, were brought into the laboratory and kept in the same cage for several months. On December 11, 1953, three deer mice (1 wild-type, 1 pink-eye, 1 silver-grey), *Peromyscus maniculatus*, from the mice genetics stocks, were placed in the cage with the two snakes. The desert bullsnake immediately seized the wild-type mouse and constricted it with a single anterior loop. As soon as the loop was secure and the mouse had relaxed, the snake released its oral grasp and moved the loop posteriorly, still maintaining its prey in a secure loop. During this movement the constricted mouse occasionally gave a reflex jerk. With very little difficulty the snake then stalked and captured the pink-eyed mouse, constricted it and proceeded to swallow his meal still holding the first mouse (wild-type) in a posterior loop. Only after the pink-eyed mouse was swallowed did it release the first victim, which was then promptly eaten. Approximately 30 minutes were consumed in the entire process during which the Pacific bullsnake appeared unconcerned. We were never able to induce him to eat. Three days later the desert bullsnake, with his usual healthy appetite, consumed the silver-grey mouse.

Certainly the development of this characteristic in two different snakes (even though they may be somewhat closely related) is of particular significance when one considers that most *Peromyscus* run in pairs and multiple trap captures are very common. It is of obvious advantage to the snake to be able to obtain, so to speak, two for the price of one.—DAVID L. JAMESON, *Department of Biology, University of Oregon, Eugene, Oregon.*

SURVIVAL OF SOME CENTRAL TEXAS FROGS UNDER NATURAL CONDITIONS.—The variation in life span of the individuals which compose the breeding populations of a species is one of the more important aspects of population dy-

namics. Very little is known about this phenomenon under natural conditions. The longest recorded life of a marked amphibian under natural conditions known to this worker is 23 months in *Rana catesbeiana* reported by Ingram and Raney (1943, *Amer. Midl. Nat.* 29: 239–41). Raney and Lachner (1947, *COPEIA* (2): 113–6) recorded 3 *Bufo terrestris* which survived two years but actual dates are not given. Jameson (in press, *Amer. Midl. Nat.*) recorded that 11 *Syrrophophus marnocki*, of 75 marked 18 months previously, were recaptured. Ryan (1954, *COPEIA* (2): 73–80) recorded adult *Rana clamitans* which survived 17 months and adult *Rana pipiens* which lived 10 months. Blair (1953, *COPEIA*, (3): 208–12) reported that 20 (11 percent) of 178 juvenile male *Bufo valliceps* lived 11 months.

The present study was carried out in 1949, 1950, and 1951 in Central Texas in two small ponds near Austin, Travis County. Each individual was marked by toe-clipping, and recoveries were noted when the pond was revisited at later dates. Three species were found in a small semi-permanent pond 6 miles north-east of Austin. This pond was collected twice in 1949 (April 19 and 24), twice in 1950 (April 16 and 23) and twice in 1951 (May 23 and June 12). These collecting nights were near the height of each year's breeding season.

Twenty-seven male and 17 female Great Plains spadefoot toads (*Scaphiopus couchi*) were marked in 2 collecting nights in 1949. Twenty-four (15♂ and 9 ♀) were recovered in 2 collecting nights in 1950 and six new males and three new females were marked. One male from the 1949 collections, three males and one female from the 1950 collections, and two unmarked males and one unmarked female were obtained in 2 nights of collecting in 1951. One of 24 male spadefoots marked on April 19, 1949 was recaptured 24 months later on May 23, 1951. One of three female spadefoots marked April 16, 1950 was recovered 13 months later on May 23, 1951.

Fourteen (8 ♂ and 6 ♀) spotted chorusfrogs (*Pseudacris clarki*) were obtained in 1949. Eight of these (6 ♂ and 2 ♀) were recovered in 1950 and four new males and six new females were marked. Only one unmarked male spotted frog was obtained in 1951. Of four male and four female spotted chorusfrogs marked on April 19, 1949, three males were recaptured on April 23, 1950, 12 months later; and one of the females was recovered 12 months later on April 16, 1950.

Six (5 ♂ and 1 ♀) narrow-mouth toads (*Microhyla olivacea*) were marked in 1949. Nine new males, four unmarked females and one marked male were obtained in 1950. *Microhyla* was not heard calling from this pond in 1951. One of two narrow-mouth toads marked on April 24, 1949 was recovered 12 months later on April 15, 1950. Three females were

TABLE I

POPULATION TURNOVER IN *Pseudacris streckeri*, AS INDICATED BY REPEATED SAMPLING

Example explanation of data: Forty frogs (33 males, 7 females) were collected on March 21, 1949. Nineteen (12 males, 7 females) of these were unmarked; eight males were from collection No. 2 (February 25, 1949); 13 males were from the original collection (January 23, 1949)

| Sample No. | Date | Sample No. | | | | | | | | | Total |
|------------|-------------------|------------|---------|---------|---------|---------|--------|--------|--------|--------|-------|
| | | (1) | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) | |
| 1 | January 23, 1949 | (27) | ... | ... | ... | ... | ... | ... | ... | ... | 21♂ |
| | | 21♂, 6♀ | ... | ... | ... | ... | ... | ... | ... | ... | 6♀ |
| 2 | February 25, 1949 | (18) | (15) | ... | ... | ... | ... | ... | ... | ... | 26♂ |
| | | 16♂, 2♀ | 10♂, 5♀ | ... | ... | ... | ... | ... | ... | ... | 7♀ |
| 3 | March 21, 1949 | (13) | (8) | (19) | ... | ... | ... | ... | ... | ... | 33♂ |
| | | 13♂, 0♀ | 8♂, 0♀ | 12♂, 7♀ | ... | ... | ... | ... | ... | ... | 7♀ |
| 4 | December 14, 1949 | (16) | (3) | (2) | (16) | ... | ... | ... | ... | ... | 28♂ |
| | | 14♂, 2♀ | 2♂, 1♀ | 1♂, 1♀ | 11♂, 5♀ | ... | ... | ... | ... | ... | 9♀ |
| 5 | January 4, 1950 | (14) | (2) | (6) | (6) | (18) | ... | ... | ... | ... | 36♂ |
| | | 12♂, 2♀ | 2♂, 0♀ | 4♂, 2♀ | 6♂, 0♀ | 12♂, 6♀ | ... | ... | ... | ... | 10♀ |
| 6 | February 3, 1950 | (9) | (6) | (2) | (4) | (11) | (14) | ... | ... | ... | 36♂ |
| | | 9♂, 0♀ | 4♂, 2♀ | 2♂, 0♀ | 3♂, 1♀ | 10♂, 1♀ | 9♂, 5♀ | ... | ... | ... | 9♀ |
| 7 | February 12, 1950 | (7) | (4) | (4) | (7) | (3) | (7) | (8) | ... | ... | 30♂ |
| | | 7♂, 0♀ | 2♂, 2♀ | 0 | 5♂, 2♀ | 3♂, 0♀ | 7♂, 0♀ | 6♂, 2♀ | ... | ... | 6♀ |
| 8 | February 18, 1951 | (13) | (1) | (5) | (1) | (1) | (8) | ... | ... | ... | 24♂ |
| | | 13♂, 0♀ | 1♂, 0♀ | 0 | 4♂, 1♀ | 1♂, 0♀ | 0 | 0 | 5♂, 3♀ | ... | 4♀ |
| 9 | March 27, 1951 | (2) | (2) | (1) | (2) | (4) | (2) | (6) | ... | ... | 11♂ |
| | | 2♂, 0♀ | 0 | 1♂, 1♀ | 0♂, 1♀ | 0 | 1♂, 1♀ | 2♂, 2♀ | 2♂, 0♀ | 3♂, 3♀ | 8♀ |

marked on this latter date, one of which was recovered one week later on April 23, 1950.

The effect of the environmental conditions on the breeding of the frogs that occur in this pond is demonstrated by the times of collection. These frogs respond to somewhat similar conditions and are frequently found breeding together. The peak of the warm spring rains in central Texas came in April in 1949 and 1950 but did not occur until June in 1951. The average monthly temperature was below 65° F in March of 1949 and 1950 and in April of 1951, but rose above 75° in April of 1949 and 1950 and in May of 1951. The general decrease in numbers of individuals is probably attributable to the increase in drouth conditions during the study. The average annual precipitation in Travis County is 34.08 inches. The annual precipitation during the study was: 1949, 36.34 inches; 1950, 25.79 inches; 1951, 28.98 inches.

A temporary rain pool 5 miles north of Austin was used to study survival in Streckers chorusfrog (*Pseudacris streckeri*). This species breeds during the cold rains which follow the periodic arrival of polar fronts during the winter months. The first breeding chorus recorded for each winter during the study was January 23, 1949, December 14, 1949 and

February 18, 1951. Forty-three males and 18 females were marked in 3 nights of collecting in the winter of 1949. Thirty-seven (26 ♂ and 11 ♀) of these were recovered in four collections in the winter of 1950, and 38 new males and 18 new females were marked. On two collecting nights in the winter of 1951, 15 males and one female from the first winters collection, eight males and four females from the second winters collection, and eight new males and six new females were marked (Table I).

In this study no particular attempt was made to collect large numbers of the chorusfrogs in the pond. In practice the collections were made by searching the bottom of the pond carefully with our lights in hopes of collecting females. Males were collected when chance brought them into the field of vision rather than by seeking out the calling individuals. However, more than one-half of the calling males are probably represented in each collection. Despite the intense concentration on the collection of females, less than half as many females (41) as males (89) were obtained during the study. The largest number of females collected on any one night was 10 on January 4, 1950. Only one female was collected twice in one season (February 3 and 12, 1950). Fifteen of 64 males collected in 1950 were

obtained four times. Streckers chorusfrog was apparently not as disturbed by the drouth conditions as were the other frogs studied—the sample sizes remain consistently high throughout the study. The low number of frogs obtained in March, 1951 is probably due to the lateness of the collection rather than actual loss of individuals. The season was delayed in 1951 by weather conditions until February and lasted only a few weeks.

Thus the male *Pseudacris streckeri* moves to temporary rain pools following cold winter rains and remains there for varying lengths of time. The females enter the pond at the same time or shortly thereafter and remain only a short time.

We may conclude that these four species, *Scaphiopus couchi*, *Pseudacris streckeri*, *Pseudacris clarki* and *Microhyla olivacea*, breed in central Texas in response to particular environmental factors. Each year's breeding population is composed of individuals that entered the pond on several of the preceding years, and which return to the same breeding pond each year. Individual spadefoot toads and Streckers chorusfrogs have returned to the same pond on three successive breeding seasons. Spotted chorus frogs and narrow-mouth toads have been recovered on 2 successive years.—DAVID L. JAMESON, Department of Biology, University of Oregon, Eugene, Oregon.

THE OCCURRENCE OF THE SNAKE GENUS *HYPSIGLENA* IN ECUADOR.—The genus *Hypsiglena* Cope has been recorded as a possible or as a doubtful member of the South American fauna on several occasions in the past, and the recent restriction of type locality for a synonym of *Hypsiglena torquata* to Guayaquil (Smith and Taylor, 1950, Univ. Kansas Sci. Bull., 33 (2): 364) seems to necessitate the inclusion of that species in a listing of Ecuadorian snakes. The preparation of a study of the fauna of Ecuador has led me to evaluate the basis for the record.

Hypsiglena torquata Guenther, as now understood, is known to range from México to Costa Rica. Smith and Taylor (1945, Bull. U. S. Nat. Mus., 187: 74) added that it extends "perhaps to Ecuador and Venezuela in South America." The record from Venezuela is based on a report by Jan (1871, Icon. Ofid., 38, pl. 1, F. 1), who listed it from Caracas. Dunn (1936, Proc. Nat. Acad. Sci., 22 (12): 695) considered Jan's locality erroneous. The recent report of the species in Colombia by Daniel (1949, Rev. fac. nac. agron., Medellín, 10 (36): 314) apparently is based on the Jan record, as no new specimens are mentioned. Insofar as I can learn, the species has never been collected in Colombia. The only other South American report is the record from Ecuador. The genus as a whole is centered in

northern México, and extends well into western United States (Tanner, 1944, Great Basin Nat., 5 (3/4): 92). There can be little doubt that it is a member of the younger element of the "Old Northern" fauna of Dunn (1931, COPEIA (3): 107). The southernmost records for the species that are validated by available specimens are in Costa Rica, and these are not particularly satisfactorily documented (Dunn, 1936, Proc. Nat. Acad. Sci., 22 (12): 694).

As mentioned above, Smith and Taylor restricted *Pseudodipsas fallax* Peters (1860, Monatsb. Akad. Berlin: 521) to Guayaquil, Ecuador, on the basis of a second specimen mentioned in the same paragraph as that in which *fallax* is named. Actually, *fallax* is a nomen nudum, for there are no diagnostic characters specifically given, and the few characters mentioned cannot be interpreted as diagnostic (i.e., ungrooved teeth, vertical pupil) for they are common to several species in unrelated genera. As Peters pointed out, he was not describing a new species at all, but he had noticed that the snake in the Berlin Museum collection represented a new species, and he already had prepared a description using the above name when he received a reprint of Guenther's work describing *Leptodeira torquata*. He immediately recognized his form as identical with Guenther's species, listed *fallax* under that name, and forgot about it, obviously not intending *fallax* to be a valid name. This is the kind of situation that led to the formation of a recommended change in the *Regles* by the Copenhagen Colloquium, for they state that, "where it is clear that a given name was not intended for use in zoological nomenclature, that name shall possess no status under either the Law of Priority or the Law of Homonymy," (Hemming, ed., 1953, Copenhagen Decisions on Zoological Nomenclature: 63, para. 114-2). While this is not yet in force, it indicates the manner in which the name should be handled, and it has been recommended that the Copenhagen Decisions be acted upon during the interim period before their final acceptance (Hemming, loc. cit.: 103, paras. 198-9). The restriction of the type locality appears to be superfluous, since the name has no legitimate status.

In addition to this, the specimen Peters used as the basis for his unavailable name was not the individual from Guayaquil. After mentioning the specimen from "America" in the Berlin Museum that he called *fallax*, he added that he "obtained" a second specimen he considered to belong to the species *Leptodeira torquata* from the Hamburg Museum. It had been determined as "*Dipsas annulata*" by Jan, and Peters disagreed with this assignment. Dr. Erna Mohr has sent me the single specimen now in the Hamburg Museum from Guayaquil, cata-

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| | Total |
|------------|-------|
| 21♂ 6♀ | |
| 26♂ 7♀ | |
| 33♂ 7♀ | |
| 28♂ 9♀ | |
| 36♂ 10♀ | |
| 36♂ 9♀ | |
| 30♂ 6♀ | |
| 24♂ 4♀ | |
| 11♂ 8♀ | |

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logged as *Dipsas annulata*, number 475, received from A. Westphalen. It is a typical *Leptodeira annulata*. It is not known if this is a second specimen from a series that originally included the one mentioned by Peters, or if the specimen that Peters examined was returned to Hamburg at a later date, and is the same individual I have seen. It might, of course, be an entirely different specimen, although the similarities in identification and collection data are strongly against the possibility. It is possible that the specimen still exists in the Berlin Museum.

This rather questionable record by Peters, then, is the sole basis for the presence of the genus in Ecuador. No additional specimens have been taken in almost 100 years from any part of the area between Ecuador and Costa Rica.

It seems satisfactory to conclude, therefore, that the genus *Hypsiglena* is not a member of the Ecuadorian, or for that matter, of the South American fauna, but is an Old Northern genus, with its southern limit in Costa Rica. The restriction of the

type locality for *Pseudodipsas fallax* Peters to Guayaquil, Ecuador, is based on a specimen which is quite possibly a member of a different species, was not assigned to *fallax* by the original author, and comes from a locality far beyond the currently recognized range of the species to which the name belongs. It is felt necessary to reject the restriction as untenable, on this evidence, and to assign Peters' specimen from Guayaquil to the species *Leptodeira annulata*, with an appropriate amount of doubt. This has the salutary effect of removing *Hypsiglena torquata* from consideration as a member of the Ecuadorian fauna. In addition, further restriction of the name *P. fallax* or of its type locality is not necessary or desirable, since the name is not validly proposed, and has no status under the current *Reglés*.

My work on the herpetofauna of Ecuador has been supported by a grant from the American Philosophical Society.—JAMES A. PETERS, Department of Biology, Brown University, Providence, Rhode Island.

Ichthyological Notes

FOOD HABITS OF THE BURBOT (*LOTA LOTA LACUSTRIS*) IN THE WHITE RIVER, A MICHIGAN TROUT STREAM.—The food habits of burbot in lakes have been studied extensively (Van Oosten and Deason, 1938, Trans. Amer. Fish. Soc., 67: 155-77; Bjorn, 1940, *ibid.*, 69: 192-6; Clemens, 1951, *ibid.*, 80: 56-66; Dymond, 1928, Publ. Ontario Fish. Res. Lab., 33: 29-41; and Cooper and Fuller, 1945, Maine Dept. Inland Fish. and Game, Fish Surv. Rept., 6: vii + 160), but very little information is available on the food habits of this fish in streams. Furthermore, almost all published data have dealt with burbot of large size (9.0" and over), although Clemens (*op. cit.*) examined 23 stomachs of small burbot (from Lake Erie); he found that gammarids and mayflies constituted a major portion of their diet.

The White River flows through White Lake and into Lake Michigan at about the mid-point of the western shore of Michigan's lower peninsula. The river and most of its tributaries are considered to be marginal trout waters (Schultz, 1953, Michigan Inst. for Fish. Res., typewritten report No. 1378). Fish collection records indicate that the burbot is one of the more abundant species in the watershed.

The present study involves stomach analyses on 196 burbot, 2.0" to 12.9" in length, from the White River and its tributaries, i.e., entirely from a stream environment. These burbot were selected from a large series of fish collections covering the entire

drainage; in this selection, samples were included for both the river and its tributaries to give good representation for the drainage as a whole. Data on the several samples are lumped for the present study. The fish were collected by a 230-volt, 11-amp, D-C shocker during the summers (May-August) of 1952 and 1953 and during February of 1954. For this study the burbot were divided into summer and winter groups, and within each seasonal grouping, into length groups as follows: 2.0"-3.9", 4.0"-6.9", 7.0"-9.9", and 10.0"-12.9". Age determinations on the burbot were not made. Items in stomach contents were counted, and volumes were determined by displacement of 80 per cent alcohol in a graduated centrifuge tube. (The oily character of stomach contents of burbot does not favor the formation of a typical meniscus if water is used.)

The 176 stomachs examined from the summer collections (25 were empty) contained a total of 46.83 ml. of food (Table I). For burbot under 7", the crustacean, *Gammarus fasciatus*, and aquatic insect larvae and nymphs were eaten most frequently, and they comprised the greatest percentages of the total food volume. *Hydropsyche* larvae and mayfly nymphs were the dominant insect forms. Among burbot over 7", gammarids and insect larvae were of less importance, while crayfish (*Cambarus*) and fish occurred more frequently. Crayfish was the most important food for the 7.0"-9.9" fish. Fish were definitely the most important

TABLE I

STOMACH CONTENTS OF *Lota lota lacustris*, WHITE RIVER WATERSHED, IN SUMMER

Figures are volume percentage of each type of food, and frequency-of-occurrence percentage for each type of food in stomachs containing food. Tr. = trace

| Length of burbot..... | 2.0"-3.9" | | 4.0"-6.9" | | 7.0"-9.9" | | 10.0"-12.9" | |
|--|-----------|------------|-----------|------------|-----------|------------|-------------|------------|
| Total volume of food (ml.)..... | 2.58 | | 11.51 | | 26.29 | | 6.45 | |
| Number of stomachs with food..... | 35 | | 68 | | 43 | | 5 | |
| Number void..... | 2 | | 8 | | 15 | | 0 | |
| Food items L = larva N = nymph | Vol. % | Freq. % | Vol. % | Freq. % | Vol. % | Freq. % | Vol. % | Freq. % |
| Annelida..... | 3.1 | 2.9 | 2.2 | 1.5 | 23.7 | 9.3 | ... | ... |
| Malacostraca..... | 32.2 | 91.4 | 27.4 | 57.4 | 32.0 | 69.8 | 22.5 | 40.0 |
| <i>Gammarus fasciatus</i> | 30.6 | 91.4 | 16.9 | 47.1 | 2.2 | 30.2 | ... | ... |
| <i>Cambarus</i> sp..... | 1.6 | 8.6 | 10.3 | 14.7 | 29.7 | 46.9 | 22.5 | 40.0 |
| Aquatic insects..... | | | | | | | | |
| Ephemeroptera ¹ (N)..... | 16.3 | 62.8 | 12.4 | 55.9 | 3.2 | 41.9 | Tr. | 20.0 |
| Trichoptera ² | 5.0 | 37.1 | 24.9 | 75.0 | 6.2 | 58.1 | Tr. | 20.0 |
| <i>Hydropsyche</i> (L)..... | 2.3 | 20.0 | 21.2 | 66.2 | 4.9 | 41.9 | ... | ... |
| Diptera ³ | 4.6 | 65.7 | 0.8 | 26.5 | 3.3 | 27.9 | 0.3 | 40.0 |
| All other aquatic insects ⁴ | 1.7 | 2.9 | 6.4 | 17.7 | 3.1 | 13.9 | 0.5 | 20.0 |
| Other invertebrates..... | ... | ... | 0.2 | 1.5 | 0.1 | 2.3 | ... | ... |
| Fish ⁵ | 3.9 | 2.9 | 1.4 | 4.4 | 12.9 | 23.2 | 72.1 | 100.0 |
| Debris ⁶ | 33.2 | ... | 24.3 | ... | 15.5 | ... | 4.6 | ... |

¹ 7 forms, mostly Baetidae and Heptageniidae.

² 5 forms, including *Brachycentrus*, *Hydropsyche* and Limnephilidae.

³ 8 forms, mostly *Simulium*, *Tendipes*, *Pentaneura*, and including Tipulidae and Chaoborinae.

⁴ Odonata, Plecoptera, Hemiptera and Coleoptera.

⁵ 7 forms: *Colinus bairdi*, brown trout, rainbow trout, blacknose dace, pearl dace, burbot, Johnny darter, and undetermined fish remains.

⁶ Inorganic and organic debris (plant and animal remains) unidentified.

food of burbot over 10.0"; blacknose dace and rainbow trout were eaten more frequently than other fish.

Although the winter sample (20 stomachs, 2 empty) was small, the analysis does show a trend. The total food volume amounted to 14.04 ml. (Table II). There were no burbot in the 2.0"-3.9" length group; presumably the smaller fish had attained a length of at least 4.0" by wintertime. For burbot in the 4.0"-6.9" length group, insect larvae (*Hydropsyche*, mayfly, and plecopteran) and *Gammarus fasciatus* were the important constituents of the winter diet, both volumetrically and by frequency of occurrence. The 7.0"-9.9" burbot fed more on gammarids during the winter, as compared to the preference for crayfish during the summer (noted above). Probably the increased consumption of gammarids during winter occurred because of an unavailability of crayfish. One fish in the 10.0"-12.9" group, collected in winter, contained fish remains.

Except for some switch from crayfish to gammarids (see above), the summer diet of burbot was similar to that of winter.

The results indicate that feeding habits of burbot in the White River are related to size of food and size of consumer. Small burbot feed on small food

TABLE II

STOMACH CONTENTS OF *Lota lota lacustris*, WHITE RIVER WATERSHED, IN WINTER

Figures are volume percentage of each type of food, and the frequency-of-occurrence percentage for each type of food in stomachs containing food

| Length of burbot ¹ | 4.0"-6.9" | | 7.0"-9.9" | |
|--------------------------------------|-----------|------------|-----------|------------|
| Total volume of food (ml.)..... | 2.9 | | 6.74 | |
| Number of stomachs with food..... | 11 | | 6 | |
| Number void..... | 2 | | 0 | |
| Food items L = larva N = nymph | Vol. % | Freq. % | Vol. % | Freq. % |
| <i>Gammarus fasciatus</i> | 23.1 | 81.8 | 77.2 | 83.3 |
| Aquatic insects..... | | | | |
| Ephemeroptera ² (N)..... | 24.5 | 100.0 | 7.0 | 83.3 |
| Plecoptera (N)..... | 9.7 | 72.7 | 1.8 | 66.7 |
| Trichoptera ³ (L)..... | 6.5 | 45.5 | 0.1 | 16.7 |
| <i>Hydropsyche</i> (L)..... | 3.8 | 36.4 | 0.1 | 16.7 |
| Diptera ⁴ | 0.7 | 27.3 | 0.1 | 16.7 |
| Debris ⁵ | 35.5 | ... | 13.8 | ... |

¹ A single burbot in the 10.0"-12.9" group contained 4.4 ml. of food which was 1.1% *Gammarus fasciatus* and 98.9% fish (Cyprinodontidae).

² 5 forms, mostly Baetidae and Heptageniidae.

³ 4 forms, *Hydropsyche*, *Brachycentrus*, Limnephilidae, and unidentified larva.

⁴ 3 forms: *Tendipes*, *Pentaneura*, and unidentified larva.

⁵ Plant and animal remains (unidentified).

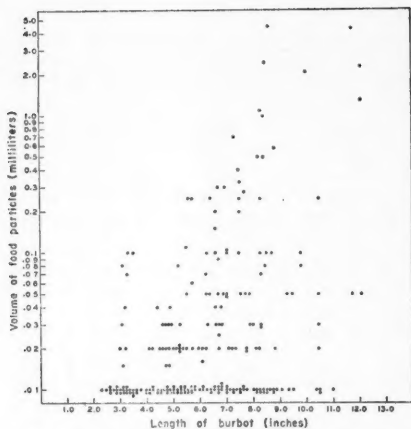


Fig. 1. Volume of individual food particles, in stomachs of burbot, plotted against the size (length in inches) of consumer.

items, and large burbot feed mostly on larger items. The sequence generally is: insects, gammarids, crayfish, and fish. The positive correlation between food size and consumer size is shown in Figure 1, where volumes of all individual food items are related to size of consumer. The correlation would be higher if the larger burbot had not taken in a few small items along with the large ones. Many other investigators have found a similar correlation between size of food and of consumer. For example, Smyly (1952, Proc. Zool. Soc. London, 122: 407-16) in his study of perch fry, and Daiber (1952, Ohio Jour. Sci., 52 (1): 35) in his study of the freshwater drum, noted such a correlation; and Odum (1953, Fundamentals of ecology, W. B. Saunders, xii + 384 pp.) stated: "Size of food is one of the main reasons underlying the existence of food chains, This is because there are usually rather definite upper and lower limits to the size of food that can efficiently support a given animal type."

As fish increase in size, they can, of course, obtain a much greater volume from a few large food items than they would obtain from a greater number of small items. No doubt there is a point of diminishing return in the relationship between the amount of effort exerted by a fish in obtaining a particular food item and the nutritional benefit obtained from it. Cooper (1941, Maine Dept. Inland Fish. and Game, Fish Surv. Rept., 4: 1-238) suggested that the number of food organisms consumed is a better index of the amount of effort on the part of the fish in seeking and capturing its food; while the volume of food is presumably a better index of the amount of benefit which the fish obtains from it.

The present collections of burbot were made by a stream survey party of the Institute for Fisheries Research. Permission to study the collections and to review the distributional records on burbot is gratefully acknowledged.—ALFRED M. BEETON, Department of Zoology, University of Michigan, Ann Arbor, Michigan. (Joint contribution with the Institute for Fisheries Research, Michigan Department of Conservation.)

AGE AND GROWTH OF THE NORTHERN HOGCHOKER, *TRINECTES MACULATUS MACULATUS*, IN THE PATUXENT RIVER, MARYLAND.—A number of investigators have studied the early growth and natural history of the northern hogchoker, *Trinectes maculatus maculatus* (Bloch and Schneider), but none has described the age and growth rate of this species. Hildebrand and Schroeder (1928, Bull. U. S. Bur. Fish., 43(1): 175-7) pointed out that spawning apparently took place during late spring and throughout the summer. Hildebrand and Cable (1938, *Ibid.*, 48: 630-40), in describing in great detail the early life history of the hogchoker from egg to juveniles of about 100 mm. in North Carolina waters, stated, "Subsequent growth remains almost entirely undetermined [sic], though among a limited number of larger specimens, measured in April (1931), there is another slight mode around 140 mm., indicating that fish approaching an age of 2 years probably are fully grown." Hildebrand and Schroeder (*op. cit.*) presented a table of measurements based on young ranging in total length from 1.3 to 4.6 inches (133 specimens) concerning which they wrote, "... quite probably were in their second summer." On the basis of age and growth analysis of the scales of 42 specimens collected in Maryland waters, this statement appears to be erroneous with regard to the age of the hogchoker at the lower size limits in Chesapeake Bay.

The specimens used in this study were collected from the lower Patuxent River and tributaries in the vicinity of the Chesapeake Biological Laboratory at Solomons, Calvert County, Maryland (Table I). They were weighed, measured, and samples of scales were taken from the approximate center of the dorsal surface of the fish slightly to either side of the lateral line. Less than half were sexed. Impressions of the scales were later made on cellulose acetate slides, and scale images were analyzed on an enlarger. The scales were aged, and length at each annulus was calculated with the aid of a nomograph. An average of the measurements of about four scales from each fish was used.

Although Cockerell (1912, Bull. U. S. Bur. Fish., 32: 171-2; and 1912, Proc. Biol. Soc. Wash., 26: 209-11) discussed the scales of the family Soleidae (Achiroidae was considered a synonym at the time),

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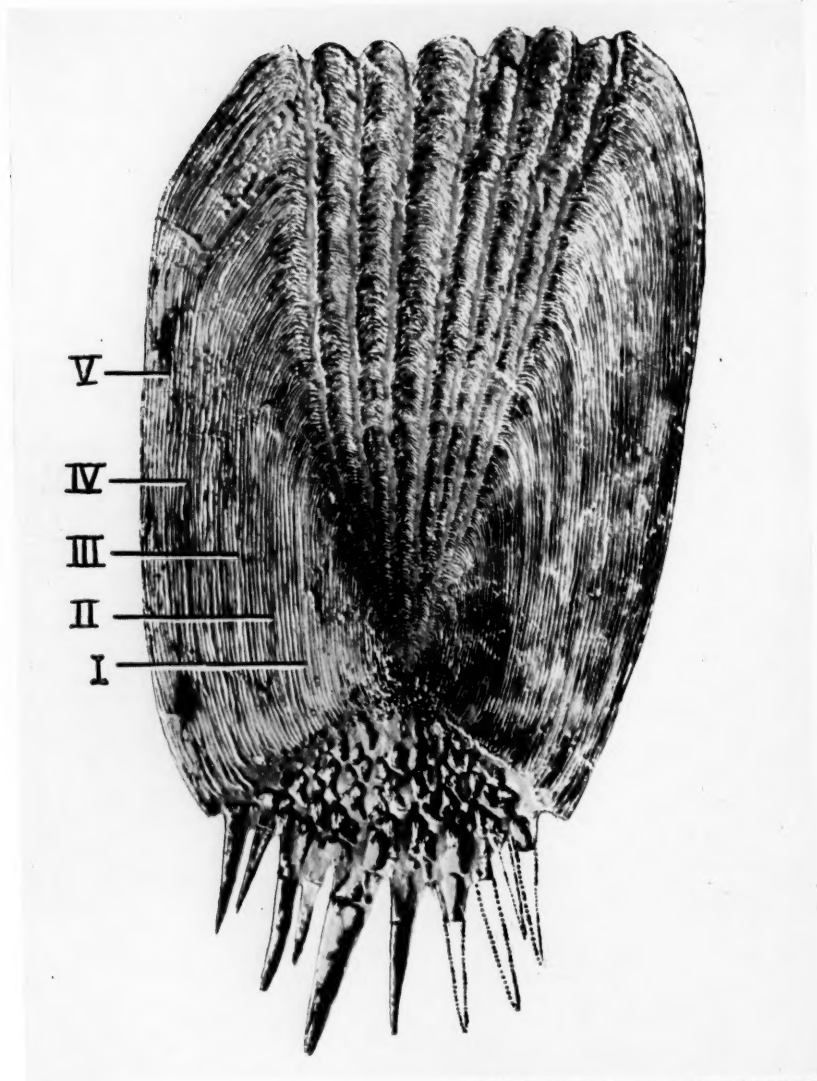


PHOTO COURTESY MICH. DEPT. CONSERVATION

Scale of the northern hogchoker, *Trinectes m. maculatus*, showing the strongly ctenoid nature of the posterior field of the scale and five annular rings. Adult female, 5.8 inches in total length, collected from Patuxent River, Maryland, August 13, 1952. Photograph retouched from plastic impression.

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TABLE I

LOCATIONS, DATES, AND CONDITIONS, UNDER WHICH HOGCHOKERS WERE TAKEN IN THE PATUXENT RIVER, MARYLAND

| Locality... | Solomons Island | Sollers Point | Point Patience | Mill Creek |
|------------------------------------|----------------------------|----------------------|----------------|--------------------|
| Date..... | V:18:50 VIII:3-5: 52 | VII:22- VIII:7:52 | VII:29: 52 | VII:23-26: 52 |
| Salinity, p.p.t..... | 13.6 | 9.0-11.0 | 10.0 | 9.4 |
| Depth at capture, in feet... | 9.0 | 8.0 | 30.0 | 8.0 |
| Type of gear..... | Seine, trap net | Seine, trap net | Trawl | Seine, trap net |
| Number of specimens... | 14 | 14 | 4 | 10 |

he did not illustrate the scales of the hogchoker. The accompanying illustration (Pl. I) reveals the strongly ctenoid nature of the posterior field of the scale. In general, the scales of most hogchokers show what appear to be true annuli. Between them, at varying distances from the annular rings, are marks that are thought to resemble the spawning rings of the scales of other species. These observations tend to support the premise that spawning may occur at various times during the summer. At the periphery of scales from fish over four years old, there is a tendency for the annuli to become progressively more closely spaced.

The scales revealed that hogchokers used in this

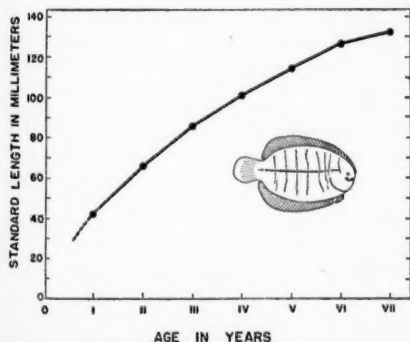


Fig. 1. Growth curve based on calculated lengths at each annulus of the northern hogchoker, *Tripterygion m. maculatus*, from the Patuxent River, Maryland.

TABLE II

MEAN CALCULATED STANDARD LENGTHS AND ANNUAL LENGTH INCREMENTS IN MILLIMETERS FOR 42 HOGCHOKERS COLLECTED IN PATUXENT RIVER, MARYLAND, DURING 1950 AND 1952

| Age group | Number of fish | Mean S.L. | Calculated length at end of year of life | | | | | | |
|---|----------------|-----------|--|-----|-----|-----|-----|-----|-----|
| | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| I | 1 | 50 | 28 | | | | | | |
| II | 3 | 92 | 45 | 78 | | | | | |
| III | 8 | 85 | 35 | 60 | 83 | | | | |
| IV | 9 | 106 | 46 | 68 | 88 | 103 | | | |
| V | 10 | 125 | 46 | 69 | 87 | 103 | 118 | | |
| VI | 8 | 136 | 39 | 60 | 78 | 96 | 111 | 126 | |
| VII | 3 | 140 | 41 | 64 | 78 | 93 | 105 | 120 | 131 |
| Grand averages and total. | 42 | ... | 40 | 66 | 82 | 98 | 111 | 123 | 131 |
| Increments of growth | | | 40 | 26 | 16 | 16 | 13 | 12 | 8 |
| Equivalent total length in inches | | | 1.9 | 3.1 | 3.9 | 4.7 | 5.3 | 5.8 | 6.3 |
| Number of fish | 42 | 41 | 38 | 30 | 21 | 11 | 3 | | |

study ranged from one to seven years of age (Fig. 1). Of these, the three-, four-, five-, and six-year-old specimens comprised 83 per cent of the total (Table II). The overall growth curve calculated on 42 specimens by the conventional aging technique showed that the annual increments were greatest during the first two years and that they leveled off slightly during the sixth year. Various investigators have indicated that hogchokers have a prolonged breeding period from spring through early autumn. A total of 20 females from the sample of 42 fish taken in August contained large ovaries with partially ripe eggs. A calculated growth curve for these females coincided almost exactly with the overall curve for the 42 specimens. Other females examined from May through autumn possessed eggs which were more or less ripe. That there must be a late brood is suggested by the size range of a number of juveniles collected by Earl Walker, biologist, Maryland Department of Research and Education, in April, 1952, at Lower Marlboro, where the water varies from fresh to 2 ppt salinity. Seven specimens ranging from 10 to 20 mm., and seven ranging from 35 to 40 mm., were taken in a trawl in water 30-40 feet deep. These were probably hatched in the autumn of 1951. Pearson (1941, Fish. Bull., U. S. Fish and Wildlife Serv., 50 (36): 84) stated that the seasonal distribution of young indicates that the hogchoker spawns largely in midsummer. Planktonic juveniles (1.5-4.0 mm.) were taken from July through September, one mile off Little Creek near the mouth of

Chesapeake Bay, Virginia. Perlmutter (1939, Suppl. to 28th Ann. Rept. New York State Conserv. Dept. for 1938 (2): 22) reported taking post-larvae (2.2–3.7 mm.) from the end of June to early July in New York waters.

It was not possible to sex all of the specimens; all that were sexed, however, were females. Inasmuch as all of those that were sexed (47 per cent of those used in the study) were taken by trap net or seine in relatively shallow water, it is believed that such gear fished selectively for females. It is probable that the preponderance of females means that prior to spawning they frequent the shoals among various types of vegetation, including: widgeon grass (*Ruppia maritima*), *Potamogeton richardsoni*, several other species of *Potamogeton*, eelgrass (*Zostera marina*), waterweed (*Anacharis canadensis*), and sea lettuce (*Ulva lactuca*). Males may frequent the deeper areas. No mention is made in the literature of the occurrence or habitat distribution of males, although Hildebrand and Cable (*op. cit.*) presumably used male fish in laboratory tanks to fertilize eggs that were spawned in the evening by females. Partially ripe females, ranging from 111 to 124 mm. in standard length, were aged as four years in the present study; this size range is slightly larger than the minimum size range of sexual maturity given as 113 to 165 mm. (in total length) by Hildebrand and Schroeder (*op. cit.*).

The length-weight relationships of the 42 specimens is indicated on Figure 2. The greatest standard length recorded was 148 mm. (5.8 inches). This is approximately two-thirds of the maximum size recorded for this species; i.e., a standard length of 212 mm. (8.3 inches), by Merriman (1939, COPEIA (2): 113). These figures can be changed by the following conversion factors calculated from 12

specimens: from standard length to total length, 1.22; from total length to standard length, 0.82.

Although the sample is inadequate to describe fully the age and growth of hogchokers, the results indicate that specimens in the study ranging from 50 to 148 mm. in standard length and from 6.0 to 123.0 g. in weight are from one to seven years old. They are sexually mature in the Patuxent River beginning at four years of age and at 111 mm. in standard length.

Appreciation is expressed to Dr. R. V. Truitt, director, and to H. J. Elser, J. Manning, and E. Walker, biologists, Maryland Department of Research and Education, for comments and suggestions in the preparation of this paper.—ROMEO MANSUETI, Maryland Department of Research and Education, Solomons, Maryland and RALPH PAULY, Biology Department, Wooster College, Wooster, Ohio.

COLOCONGER RANICEPS IN THE GULF OF MEXICO.—Among the fishes discovered by the INVESTIGATOR in the Indian Ocean were several specimens of a unique genus and species of congrid eel for which Alcock proposed the name *Coloconger raniceps* (Alcock, 1889, Ann. Mag. Nat. Hist., ser. 6, (4): 456; 1892, Illust. of the Zool. of H.M. Indian Mar. Surv. Steam. Investigator . . . , pt. 1—Fishes, pl. 7, fig. 4). His specimens were taken off Ross Island in the Andaman Sea at a depth of 265–271 fathoms. Additional specimens were reported by Lloyd (1909, Mem. Indian Mus., 2 (3): 152), Sewell (1912, Rec. Indian Mus., 7 (1): 12), Brauer (1906, Wiss. Ergeb. Deutschen Tiefsee-exped. . . "Valdivia", 15 (1): 123, pl. 8, fig. 1), and Norman (1939, Rep. John Murray Exped., 7 (1): 42)—all from deep water of the Indian Ocean. More recently a specimen taken at a depth of 300 meters in Suruga Bay, Japan, was discussed by Kuronuma (1940, Dobutugaku Zassi, 52 (10): 405). It was therefore of interest to find among the collections made by the M. V. OREGON, research vessel of the U. S. Fish and Wildlife Service, two specimens clearly referable to Alcock's genus *Coloconger*. Although these specimens are not wholly in accord with the original and subsequent descriptions of *C. raniceps*, the differences are but little greater than those apparent in the descriptions of the Indian Ocean collections. The two Gulf of Mexico specimens discussed below are therefore tentatively referred to Alcock's Indian Ocean species.

The description which follows is based on two specimens collected at OREGON Station No. 1019: Lat. 24° 16' N., Long. 83° 22' W. (Gulf of Mexico, off Tortugas, Florida); 40-foot shrimp trawl dragged over a mud bottom for two hours at a depth of 375 fathoms.

Head and body compressed. Body tapering evenly from the point of greatest depth, at origin of dorsal

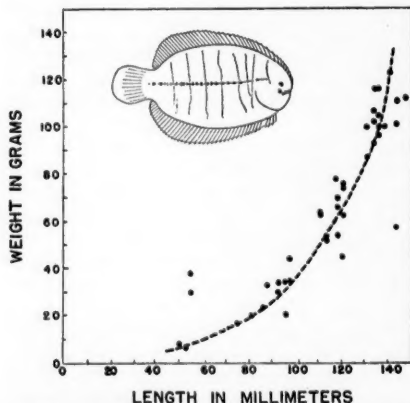


Fig. 2. Length-weight relationship of 42 specimens of the northern hogchoker, *Trinectes m. maculatus*, from the Patuxent River, Maryland.

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A specimen of *Coloconger raniceps*, 279 mm. in standard length, from the Gulf of Mexico

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fin, to the pointed caudal. No scales. Head massive, 5.5 to 6.6 in standard length. The nostrils, sensory and mucous pores, and large eye, conspicuous. Snout bluntly rounded, terminal in the larger specimen and coterminous with lower jaw in the smaller. Anterior nostril large, tubular, entering a large nostril cavity and on a horizontal with lower edge of eye. Surrounding each anterior nostril and connecting with the nasal cavity are four or five tubular pores comparable in diameter to those of the anterior end of the lateral line. Posterior nostril level with middle of eye, with a fleshy tab anteriorly, and equal in diameter to the anterior nostril. Eye large, its horizontal axis longer than its vertical. Dermal covering of eye continuous with that of head and without pores or dermal accessories. Horizontal diameter of eye 2.9 to 3.6 in head, equal to the convex interorbital.

Lower jaw rounded and subterminal in the larger fish, pointed and coterminous with snout in the smaller. Angle of gape under posterior edge of pupil. Tongue toothless and free anteriorly. Upper jaw with a narrow band of conical teeth anteriorly; a single row laterally. Minute, stiffened dermal papillae on both lips. Lower jaw with a single row of closely set, compressed teeth. Vomer and palatines toothless.

Gill opening restricted, its vertical length about equal to diameter of pupil. Gill flap attached dorsally at mid-pectoral base. Pectoral fin well developed, of 20 or 21 rays. Length of pectoral 1.8 to 2.0 in length of head. Dorsal and anal fins well developed, confluent. Rays slender, about 198 to 212 in dorsal; 110 to 125 in anal. Dorsal fin originates behind pectoral base; distance from snout 4.4 to 5.3 in standard length. Greatest height of dorsal about equal to vertical diameter of eye, higher than anal. Anal originating immediately behind anus; snout to anal origin 1.5 to 1.6 in standard length. Pectoral, dorsal, and anal fins covered with skin.

Lateral line commencing on head, behind dorsal margin of eye, and terminating at base of caudal fin. Lateral line tube pierced anteriorly by pores, each of which bears a black tubule. Posteriorly, the lateral line tube is open in both specimens, although this may be attributed to the abrasive action of the trawl. There are about 74 pores anterior to the level of the anus. Those posterior to it cannot be accurately counted but number about 66. Pores similar to these lateral-line pores occur on the nape and head, and accessory lateral-line systems are evident behind and below the eye and on the rami of the lower jaw.

Measurements, expressed in percent of standard length, of the larger (279 mm. in standard length) specimen followed, in parentheses, by those of the smaller (147 mm.): head length (to upper end of

gill opening), 18.3 (15.6); snout, 4.3 (3.7); horizontal diameter of eye, 5.0 (5.4); vertical diameter of eye, 4.1 (4.4); fleshy interorbital, 4.7 (5.4); post-orbital, 9.3 (8.5); length of upper jaw, 8.6 (10.9); length of mandible, 8.2 (10.9); greatest width of head, 8.6 (6.8); greatest depth of head, 9.3 (8.8); greatest depth of body, 14.0 (10.2); snout to origin of dorsal fin, 22.9 (18.7); snout to upper end of base of pectoral, 17.9 (17.0); snout to origin of anal fin, 62.4 (66.7); length of pectoral, 10.0 (7.5); length of mid-caudal ray, 3.8 (3.4).

The more massive head, larger eye and narrower interorbital, the more posteriorly placed dorsal fin, and the pattern and number of sensory pores distinguish our specimens from those described by Brauer and Norman, and, to a lesser degree, from those of Alcock and Kurokuma. Since morphometric data for the several Indian Ocean specimens have not been published, no evaluation of the variation attributable to sex and growth can be made. The difference in proportions between our larger and smaller specimens suggests that growth changes are significant. It is best, therefore, to postpone a detailed systematic analysis of *Coloconger* material from the three oceans can be directly compared and to consider our specimens American representatives of *Coloconger raniceps*.—GILES W. MEAD, U. S. Fish and Wildlife Service, Woods Hole, Massachusetts and JOHN NICHOLSON, Woods Hole Oceanographic Institute, Woods Hole, Massachusetts.

THE NAME OF THE SOUTH AMERICAN CLUPEID FISH, *PRISTIGASTER*.—The little South American fresh-water herring, *Pristigaster*, has aroused the interest of some ichthyologists because of its similarity in form to the South American gasteropelecina flying fishes. The species has seldom been seen and relatively few specimens exist in museums. The fish occurs in Guiana streams and in the Amazon, running far up into the Peruvian tributaries of that river.

While recently giving a last look at the late Dr. Hildebrand's clupeid manuscript for "Fishes of the Western North Atlantic," I became aware that the early synonymy of the single known species of *Pristigaster* has never been properly set forth, and that confusion has existed in regard to the correct specific name. An attempt is made here to clarify the situation, and I quote the pertinent older references, several of which (especially the Cuvierian figures) have been overlooked.

Pristigaster Cuvier, 1817

Pristigaster Cuvier, 1817, *Regne Animal*, ed. 1, 2: 176 and 4: pl. 10, fig. 3 (type species, by monotypy, not specifically named, but it is figured and this same figure is repeated in the second edition of the *Regne Animal* in which a specific

name is given; type by monotypy therefore is *P. cayanus* Cuvier, 1829).

There is little problem in regard to the generic name except its date. It must be accepted under the International Rules as of 1817, for the genus was described at that time (really a generic and specific description combined), with a single species (locality "Mers d'America") referred to it. The species was even figured by Cuvier in 1817, a fact overlooked by ichthyologists. That a specific name was not provided until 1829 has no effect on the acceptance of the name as of 1817, under the Rules.

Pristigaster cayana Cuvier, 1829

Pristigaster Cuvier, 1817, *Regne Animal*, ed. 1, 2: 176 and 4: pl. 10, fig. 3 (description; no specific name given; type locality "Seas of America").—Cuvier, 1830, *Regne Animal*, ed. 2, 3: pl. 12, fig. 3 (specific name not given on plate but present in text; see Cuvier, 1829, below).

Pristigaster cayanus Cuvier, 1829, *Regne Animal*, ed. 2, 2: 321 (name only, in footnote, but identity with the figured American *Pristigaster* of 1817 is obvious, not only because of the identical 1830 figure referred to above but also because the only other species referred to the genus is from India; type locality fixed by the specific name as Cayenne, French Guiana).—(Cuvier and) Valenciennes, 1847, *Hist. Nat. Poiss.*, 20: 334, pl. 597 (description).

Pristigaster martii Agassiz, 1829, in Spix, *Genera Species Piscium* Brazil.: 55, pl. 24a (type locality "mouth of the Amazon").

Pristigaster americanus Guérin-Ménéville, 1829–1844, *Iconographie Regne Animal de Cuvier* (Mamm., Ois., Rept., Poiss.): 33, pl. 57, fig. 3 (type locality "coasts of South America in the Atlantic").

The specific names *P. cayanus* and *P. martii* have both been used for this species, for both were proposed in the same year (1829) and it seems impossible at this late date to determine whether the work of Cuvier or that of Spix and Agassiz has actual priority in publication date. Internal evidence in both works, as well as the known historical fact that Agassiz prepared the Spix volume for publication in the laboratories of the Jardin des Plantes in Paris, which were presided over by Cuvier, indicates that each author was aware of the other's manuscript before publication. Their material was not, however, identical. Cuvier's was from Cayenne, as his specific name indicates. Agassiz's specimens were collected by Spix in Brazil. However, the apparent belief of some ichthyologists that Cuvier's *P. cayanus* was a *nomen nudum* as of 1829 shows insufficient acquaintance with the literature; he was clearly providing a specific name for a species which he had already both described and figured in 1817. That no formal "specific" description (as distinguished from a "generic" description) was given in 1817 is immaterial. Who can

say with surety what are generic and what are specific characters, especially in a monotypic genus? Besides, Cuvier figured the species in 1817, which is sufficient description under the Rules for species described up to the end of 1930.

The name *P. americanus* seems to have been overlooked by all ichthyologists. The dates of the livraisons of Guérin-Ménéville's work (the copy kindly lent me by Dr. J. C. Briggs) are not apparent from the work itself. They were apparently reviewed as they appeared in Ferussac's *Bulletin*, but that journal is not available to me. The name is undoubtedly of later date than those of Cuvier and Agassiz, and there seems little point in worrying over it.

The name *cayanus* has been preferred over *martii* by most subsequent writers, including both Valenciennes and Günther. I am therefore retaining it. However, the Greek term *gaster* (meaning belly) is of feminine gender, and the Rules require that the specific name agree in gender. It must, therefore, be *cayana*. Incidentally, if *martii* were to be accepted, the present Rules would apparently require that it be changed to *martiusi*, for the name was given in honor of Spix's distinguished co-traveller, Martius.—GEORGE S. MYERS, *Natural History Museum, Stanford University, California*.

THE WHITE SEA BASS, *CYNOSCION NOBILIS*, IN PUGET SOUND.—Because of the interest of ichthyologists, climatologists, and others in the northward distribution of warm-water fishes along our Pacific Coast, we are noting another occurrence of the white sea bass, *Cynoscion nobilis* (Ayres), in the Puget Sound region. On January 21, 1955, Mr. Raymond O. Watne and Mr. James K. Stanford of Seattle, while crab-fishing off the mouth of the Stillaguamish River between Camano Island and the mainland, in water about 15 feet deep, encountered a large fish swimming at the surface in such a feeble condition that they were able to catch it with their hands. Ashore, it weighed 42 pounds. An observer identified it as a "Mexican sea bass" with which he was familiar farther south. A friend, Mr. William J. Kasper, took three 35-mm. color flash pictures of the unusual fish. Although the specimen was not preserved, the pictures were brought in for identification, on March 2, 1955, and are on file at our laboratory.

The fish was encountered under conditions remarkably similar to those of the first record of this species from the Strait of Juan de Fuca. Clemens and Wilby (1946, *Fish. Res. Bd. Canada*, Bull. 68: 146) related that in January, 1893 at Sooke, a 45-pound specimen was discovered floating, and that a second individual was obtained on July 15, 1906, in a fish trap at Sherringham Point. The pres-

ent, third record for the Puget Sound region represents an additional range extension of approximately 100 miles.—KELSHAW BONHAM AND PAUL R. OLSON, *Applied Fisheries Laboratory, University of Washington, Seattle, Washington.*

LEPIDOCYBIUM FLAVOBRUNNEUM, A RARE GEMPYLID FISH NEW TO THE FAUNA OF THE GULF OF MEXICO.—The motor vessel MIKE FLECHAS caught a fish on a tuna long-line set off Mississippi, 120 miles south of Horn Island Sea Buoy on the night of January 13, 1955 at a depth of about 30 fathoms. This specimen has been assigned USNM No. 164013. Captain Charles Kaufmann brought the fish to Stewart Springer who immediately recognized its similarity to *Ruvettus*, the oilfish, but also its differences and tentatively identified it with *Lepidocybium flavobrunneum*, which name now has been verified as correct.

This specimen, after preservation, measured 1,210 mm. forked length, and 1,290 mm. total length which makes it the longest so far recorded for the species. Other measurements in mm. are: head, 300; greatest depth, 235; snout, 130; eye, horizontal diameter, 40, vertical, 55; length of maxillary, 135; length of pectoral, 170; snout to origin of spiny dorsal, 345, to soft dorsal, 625, to anal, 750. The dorsal rays are IX-17 + 6 finlets; anal II, 13 + 4 finlets; pectoral 17; pelvics I, 5; gill rakers, represented by rough low tubercles, 0 + 1 + 5 on first gill arch. We cannot find any trace of a lateral line.

We have studied this large fish, the only specimen in the National collections, and have compared it with descriptions in the literature. Dr. Ian S. R. Munro (1949, Proc. Roy. Soc. Queensland, 60 (3): 31-41, figs. 1-3, pl. 1, figs. 1, 2) has described *L. flavobrunneum* (Smith) so fully that we can add little to his thorough treatment. A few papers have appeared, since Munro published in 1949, as follows: Beaufort, in Beaufort and Chapman (1951, The Fishes of the Indo-Australian Archipelago, 9: 215) incorrectly placed *Nesogrammus thompsoni* Fowler (actually a synonym of *flavobrunneum*) as a synonym of *Grammatocorynis bicarinatus*

(Quoy and Gaimard) since the latter is a different genus and species; Smith, J. L. B. (1949, The Sea Fishes of South Africa, p. 310, fig. 862); Matsubara and Iwai (1952, Pacific Sci., 6 (3): 195 [Key to genera of Gempylidae]); and Grey (1953, COPEIA (3): 138-9 [Key to genera and species of Gempylidae]) briefly discussed *L. flavobrunneum*.

Lepidocybium flavobrunneum (Smith) was previously known from only 10 specimens, originally recorded as follows in the literature: *Cybium flavobrunneum* Smith (Illustration of the Zoology of South Africa, 4, pl. 20, 1849) from Cape of Good Hope; *Xenogramma carinatum* Waite (Rec. Australian Mus., 5 (3): 158, pl. 19, fig. 1, 1904) from Lord Howe Island; also under same name: Myers (1932, Trans. San Diego Soc. Nat. Hist., 7 (11): 111-8, pl. 7) from Long Beach, California; Kamohara (1938, Annot. Zool. Japonensis, 17 (1): 46, pl. 3, fig. 1) from Tosa, Japan; Nichols and La Monte (1943, COPEIA, (1): 50) from 25 miles off Cabo Blanco, Peru at over 100 fathoms depth. Munro (1949, Proc. Roy. Soc. Queensland, 60 (3): 31, pl. 1) reported *L. flavobrunneum* from Nelsons Bay, Port Stephens, Australia; *Lepidosarda retigramma* Kishinouye (1926, Jour. College Agri., Univ. Tokyo, 7: 278, figs. 1-3) from Owase, Miyeken, off Pacific coast of the middle of Hondo, Japan; *Nesogrammus thompsoni* Fowler (1923, Occas. Pap. B. P. Bishop Mus., 8 (7): 376-8) from Honolulu.

All of the above 8 records are from the Indo-Pacific, whereas the following two are Atlantic: *Diplogonurus maderensis* Noronha (Ann. Carnegie Mus., 16 (3-4): 381, 1926) from Cama de Lobos, Madeira Islands, probably at a depth of 400 fathoms; *Thyrstites niger* Poey (Enumeratio piscium Cubensium, Pt. 1, and Anal Soc. Esp. Hist. Nat., 4: 148 (p. 74 in reprint), pl. 7, figs. 20-21, 1875) based on caudal peduncle and scales taken near Habana, Cuba.

Our specimen, the eleventh, represents the third record for the Atlantic and the first record for the Mainland of North America, extending the range to the Gulf of Mexico.—LEONARD P. SCHULTZ, *Smithsonian Institution*, and STEWART SPRINGER, *U. S. Fish and Wildlife Service, Washington, D. C.*

REVIEWS AND COMMENTS

FISHES OF JAPAN. Illustrations and Descriptions of the Fishes of Japan. By Yaichiro Okada. Maruzen Co., Ltd., Tokyo: 1 + 1-434 + 1-28, 391 figs. \$10.00.—After long delays Yaichiro Okada, who is well and favorably known personally as well as professionally to many vertebrate zoologists of America, has put out this much needed treatment in English of a large number of representative Japanese fishes. For each of the 391 species figured—roughly constituting one-third of the known rich fish fauna of Japan—there is given a rather streamlined description plus, with rare exceptions, a few to rather many natural history statements, covering such items as distribution, ecology, life history, and utilization (all under the heading of Habits). Much of this information, some very interesting, has previously been available to few occidental scientists, and constitutes perhaps the highest technical value of the book outside Japan. There, it may serve as an identification guide as well as a source of information. It treats most of the fishes that one might catch by angling in the fresh or salt waters of Japan as well as most of the species that one is apt to see in the fish markets, which are famous for their rich representation of the whole fauna. Naturalists visiting Japan will find this book useful and students will find in it a fair portrayal of the Japanese fish fauna. In most groups the excellent figures (in part original and in part judiciously copied from the technical literature) will suffice for identification—provided one turns enough pages. In the tradition of Japanese natural history books there are no keys, no tables of differences, no group descriptions, nor any other device to shortcut identification. Only occasionally are comparative notes offered for the distinction of related species that are neither described nor pictured. Typographical and other errors are not glaring. Two bad slips in the figures were noted: the figures for species 272 and 274 are transposed; a figure of a *Pseudorhombus* masquerades over the account of *Pleuronichthys cornutus*. In general, however, the publication bespeaks care, attention to detail, and thoroughness in preparation. The English is clear and concise; occasional peculiarities of expression (to an occidental) are quaint rather than confusing. In this age of increasing publication in languages not using the Latin alphabet, we are grateful to Dr. Okada for the preparation of this treatise in English.—CARL L. HUBBS, *Scripps Institution of Oceanography, University of California, La Jolla, California*.

SOME JAPANESE BOOKS ON FISHES.—The following brief summaries are intended to pro-

vide information on several Japanese books on fishes published since the war. The titles (some of them in English) of these works may arouse the American reader's interest, but the Japanese text usually bars him from forming any clear idea of their content and value.

FISH MORPHOLOGY AND HIERARCHY (the author's English title), by Professor Kiyomatsu Matsubara of Kyoto University, is a beautifully made book of 789 pages, published in 1955. Despite the title, it is entirely in Japanese. It is essentially an enlarged version of *Keys to the Fishes and Fish-like Animals of Japan* (Tokyo, 1938, Sansaidō pub.), by the same author with Yaichiro Okada, but the system of classification has been changed and the bibliographical sections have been amplified on the basis of a thorough survey of work published during and since the war. The contents include: a 59-page account of the history of the classification of fishes, divided into pre-1940 and post-1940 periods, with a deep bow to Berg's *Classification of Fishes*, which Matsubara regards as marking an epoch; 9 pages on the morphological features, measurements, and meristic counts necessary for using the keys; 5 pages of instructions on collecting, preserving, and labelling specimens; and 8 pages listing the taxonomic categories employed with their Japanese equivalents. The body of the work consists of keys to all of the fishes reported from Japan, the Kuriles, southern Sakhalin, Korea, the Ryukyus, and Formosa up to the end of 1954. These keys, unlike those in the earlier work, are accompanied by discussions of the morphology, relationships, and classification of each of the major groups. A list of selected references is provided for each Order. Nearly 300 small figures, mostly of anatomical details, copied from many sources, illustrate the text. This book is called Part I; Part II, as yet unpublished, will consist of plates of representative fishes of each group, a vocabulary, the index, and a list of general references. The book is published by the Ishizaki Shoten, of Tokyo, and Part I sells for \$14. The U. S. agent is the Charles E. Tuttle Co., Rutland, Vermont.

BIBLIOGRAPHY OF FISHES IN JAPAN, by Yaichiro Okada and Kiyomatsu Matsubara, published in 1953 by the Faculty of Fisheries of the Prefectural University of Mie, is another book with an English title and a largely Japanese content. It is a listing by years and alphabetically by author of literature dealing with the fishes of Japan from 1612 through 1950, without annotations or index. Its 228

pages include 7,200 items, many of which are actually papers on fishes of areas other than Japan or general papers on fish physiology, ecology, etc. by Japanese authors. The brief introduction does not state criteria for the inclusion of items, and the title is ambiguous. The authors do say, however, that they have tried to include all material on classification, morphology, physiology, ecology, and genetics; almost everything on fisheries and fish-culture; and comparatively little on processing technology. One wonders whether a more accurate title might not have been "A catalogue of the fish literature in some collections in Japan."

GYORUIGAKU (Ichthyology) by Professor Yasuo Suyehiro of Tokyo University, published by Iwanami Shoten in 1951, 332 pages, is entirely in Japanese. It is in the nature of a general textbook of ichthyology, with its material and illustrations drawn from a very wide variety of sources. The author's avowed purpose was to present all of the fields of ichthyology, except systematics, as broadly and in as much detail as possible. After an introductory section which defines the subject and treats briefly of the evolution, classification, nomenclature, collecting, and rearing of fishes, the main divisions of the work take up morphology, ecology, physiology, and pathology. The book is closely organized and thoroughly indexed, and if the author's desire to include absolutely everything has resulted in his giving an impression of superficiality in his treatment, the comprehensive lists of references (most of them non-Japanese) at the end of each section should enable the reader to find more detailed information if he requires it. This would seem to be an excellent textbook for the Japanese fishery schools and a good introductory text for university students. The author, incidentally, has followed the laudable practice of giving the English equivalents immediately after all Japanese technical terms, which makes the book a valuable reference for anyone reading or translating fishery Japanese.

SUISAN SHIGENGAKU SÖREN (General Treatise on the Study of Aquatic Populations), by Professor Hiroaki Aikawa of Kyushu University, 545 pages, published in 1949 by the Sangyo Tosho Company, is another eclectic work, drawing on a list of 782 references, about half of them American and European, for examples, data, and illustrations for its presentation of fishery population dynamics. Its major divisions cover the ecology of populations, factors controlling fishing grounds, methods of population study, laws governing fluctuations in the size of populations, and the effects of human activities on aquatic populations. There are separate sections on each of the major Japanese fisheries and a concluding chapter discusses the strategy of

factory ship operations. The work appears to bring together a wealth of reference material on age determination, tagging, spawning, growth, fishery management, catch prediction, and many other subjects, but to offer little that is original. The index provides a valuable set of Japanese and English equivalents for technical terms.—W. G. Van Campen, P.O. Box 3830, Honolulu, Hawaii

RYBY OKHOTSKOGO MORIA (Fishes of the Okhotsk Sea). By P. IU. Shmidt. Academia nauk SSSR, Trudy Tikhookeanskogo Komiteta VI, Moscow, 1950: 370 pp., 51 figs., frontisp., 20 plates, errata sheet inserted. (In Russian.) Published posthumously.—Most of this work was completed in 1938 and publication was scheduled for 1941. However, due to the war, publication did not again seem likely until 1947 at which time Shmidt made some changes in an attempt to bring the work up to date. The recency of publication belies the period covered by the data.

A "history of the investigations on the fauna of the Okhotsk Sea" follows the table of contents, introduction and table of abbreviations. Next is the phylogenetic listing and discussion of the species, the major portion of the text. A very brief synonymy which includes only the more important works is given for each form. Except for new forms, the species are not characterized. The discussion consists of general notes which may compare some confusing species but more often refers only to miscellaneous data on vertical distribution, temperature preferences and particular morphological features.

Included are 271 forms of marine fishes which represent 255 species in 135 genera. The following new species and subspecies are described: Bathylagidae — *Bathylagus arae*; Zoarcidae — *Lycodes brevipes ochotensis*, *L. microlepidotus*, *L. palearis multifasciatus*, *L. knipowitschi panthera*, *L. bathybius*, *Lycenchelys hippopotamus*, *Lycodapus microchir*, *Lycogramma soldatovi*; Liparidae — *Liparis l. latifrons*, *L. latifrons meridionalis*, *L. punctatus*, *L. marmoratus*, *Careproctus seraphimae*, *C. melanuroides*, *C. cypseluroides*, *C. macrodiscus*, *C. rastrinoides*, *C. nigricans*, *Paraliparis grandis*, *P. dactyloides*, and *P. albeolus*. Some of the new species have been referred to in Soviet literature since 1935 and thus were *nomina nuda*. It is unfortunate that Shmidt neither designates type specimens nor lists type localities. The possibility thus exists of serious confusion in such complex groups as the Liparidae and Zoarcidae. The task of the reviser will be made easier should the Russians publish a list of Shmidt's type material.

Of special interest is the marine cyprinid, *Leuciscus brandtii*, which is widely distributed in the southwestern Sea of Okhotsk and the northern

portion of the Sea of Japan, often far from the mouths of rivers.

Keys are given only to the species of *Lycodes* (including species from the Bering Sea), *Lycenchelys*, *Arctiellus*, *Gymnocanthus* and *Porocottus*. The *Handbook for the Identification of Fishes of the Soviet Far East and Adjacent Waters* (A. J. Taranets, 1937) has keys to all but the new species of Okhotsk fishes and thus is a useful companion volume.

Next is a "review of the status and distribution of the ichthyofauna of the Sea of Okhotsk." This is discussed at the level of family, less often subfamily and order. The schematic distribution charts are very illustrative and should be helpful to those engaged in studies of comparative distribution. Shmidt divides the waters of the North Pacific into five classes (pp. 283-89) on the basis of summer and winter surface temperature, temperature at 200 meters, annual surface variation and summer vertical variation at 200 meters: 1, tropical waters (maximal warmth); 2, warm subtropical water; 3, temperate cold water; 4, cold water; and 5, maximal cold water. The Sea of Okhotsk belongs to classes 4 and 5.

The final three chapters are: "the origin of the fish fauna of the Okhotsk Sea," "the fish fauna of the Okhotsk Sea and the Arctic Ichthyofauna" and the "conclusions." The last does little to summarize the work but considers instead regions for future study and the importance of such studies in opening new fisheries and providing food products for the Soviets. An extensive bibliography (pp. 337-51), the plates, and an index to scientific names complete the work. The reproduction of plates and text is of high quality.

The zoogeographic discussion merits attention. The reader would do well to refer also to Shmidt's *Fishes of the Pacific Ocean* (1948) since this represents, despite its earlier publication date, later thinking on this subject by him. Throughout, Shmidt considers the Okhotsk Sea as the center of evolution and dispersal for the fishes of the northern North Pacific, Arctic and North Atlantic (in part) Oceans. This is based on his concept that the evolutionary center possesses the greatest variety of forms within a given group. He has overlooked the possibility that the richness of the Okhotsk fauna may depend on Arctic forms which dispersed southward with each glacial advance followed by isolation and differentiation in the isolated cold waters of the northern Okhotsk Sea during the interglacial periods. A glance at the geographic position of the Okhotsk Sea shows that it opens to the Pacific only at its southern and warmer end. Cold-water fishes retreating northward would be trapped at the blind end of the Sea. The Arctic members of the Okhotsk fauna, as expected, are restricted to its

northern and western portions. This strongly supports the alternate origin of the rich fauna, the survival and differentiation of glacial relicts; such an explanation seems more plausible to the reviewers. Another reason for disputing Shmidt's hypothesis of an Okhotsk origin of the Arctic fauna is the absence from the Sea of Okhotsk of such characteristic Arctic genera and species as *Arctogadus*, *Boreogadus*, *Icelus bicornis*, *Arctiellus scaber*, *Liparis koefoedi*, *Myoxocephalus quadricornis* and *Aspidophoroides olriki*. Reasons for their absence and a general discussion of this question is treated by Walters (Bull. Amer. Mus. Nat. Hist., 1955, vol. 106, art. 5).

With the appearance of this book many valuable data on a region of great zoogeographic interest, little known previously, become available to Western students. It will undoubtedly prove of great value to workers interested in the fauna of the Pacific Coast of North America. It is hoped that future publication of G. I. U. Lindberg's doctorate, *The Ichthyofauna of the Sea of Japan and its Origin*, will clarify some of the existing taxonomic and zoogeographical problems in this area and the area southwest of the Sea of Okhotsk.—VLADIMIR WALTERS AND C. RICHARD ROBINS, *The American Museum of Natural History, New York City, and the Department of Conservation, Cornell University, Ithaca, New York.*

ELEMENTS OF ECOLOGY. By George L. Clarke. John Wiley & Sons, Inc., N. Y., 1954: xiv + 534 pp., illus. \$7.50.—This recent addition to the growing number of ecology texts is organized in 13 chapters including: 1 viewpoint of modern ecology, 2 the medium, 3 the substratum, 4 water, 5 temperature, 6 light, 7 oxygen and carbon dioxide, 8 nutrients, 9 relations within the species, 10 relations between species, 11 the community, 12 succession and fluctuation and 13 dynamics of the ecosystem. References cited are listed on 17-½ pages at the end. They are heavily weighted to North American works. Illustrations are used liberally and, in general, are well chosen and well executed. There is a subject index.

Partially because of Dr. Clarke's own interests, partially because of their appropriateness and partially because of the importance of the oceans in the ecology of the Earth, many examples are drawn from the marine environment. Ichthyological examples are common throughout the text. This is not true of herpetological examples.

"Elements of Ecology" must be classified in general as a descriptive rather than an analytical text. This is perhaps as it should be. Dr. Clarke states that "The purpose of this book is to bring together in one place and in a simple way the elements of

ecology with special emphasis on the modern viewpoint of the science," and "The book is written primarily for students in ecology." In my opinion, Dr. Clarke has well fulfilled his stated objectives.—JOHN C. MARR, *U. S. Fish and Wildlife Service, P.O. Box 271, La Jolla, California.*

FROGS OF SOUTHEASTERN BRAZIL.

By Doris M. Cochran. U. S. National Museum Bulletin No. 206, 1954 (1955): xvi + 423, 34 pls. (\$2.00 from Supt. of Documents, G.P.O., Washington 25, D. C.)—Frogs (and toads) are not easy to classify or identify at best, and those of South America are not only more varied but also less well collected and studied than those of any other continent. To make matters worse, generic or group revisions are few and—save for Müller and Hellmich's Chaco report and Miranda-Ribeiro's incomplete and outdated pioneer work on the Brazilian fauna—there have been no modern well illustrated systematic monographs of the frogs of any considerable geographical segment of the continent. The result has been an enveloping cloud of taxonomic chaos that has to be experienced to be believed, that has often bogged down even those relatively few careful herpetologists who have worked with the fauna and provided a name-manufacturing field-day for some of the less inhibited ones, and that has made the secure identification of all but a minority of well known species a most uncertain business.

For these reasons it is a vast understatement to say that Dr. Cochran's carefully done monograph of the frogs of the Brazilian states of Rio de Janeiro, São Paulo and Minas Gerais is exceptionally welcome. The work has been in preparation for many years, the author has seen many of the species in the field, and she had the benefit of the active help of the late Dr. Adolpho Lutz (to whom the volume is dedicated), of his eminent daughter, Miss Bertha Lutz, and of their assistant, Joaquim Venancio, who though un-lettered is perhaps the world's most acute and able field student of frogs. In addition, Dr. Cochran has examined many of the types in European and American museums. The work is well illustrated, not only by photos of museum examples (often types) but also by the author's own drawings. A single specimen is described minutely for each species, a statistical table of six selected measurements is given for most forms, and the results are graphed in a special section—a welcome break away from routine frog systematics. Moreover, the careful description of the method of measurement (p. xiv) will serve as a model for other frog systematists.

The reviewer (see Myers, 1950, *Copeia* (3): 206; also Schmidt, 1955, "Herpetology," in *A*

Century of Progress in the Natural Sciences: 610) again decries the absence of *species* descriptions, which continues to be a major failing in many American herpetological works. Dr. Cochran herself says (p. xv) that "every physical character found in frogs varies to some extent", but her detailed description of one specimen of each form, even when reinforced with tables of variation in six proportions, gives no variational information for most of the characters described.

Another criticism also applies equally to many other herpetological papers which deal with poorly studied faunas in which many future changes in generic limits may confidently be expected—a failure to recognize the importance of citing all pertinent generic synonyms, *with not only their generic types but also the method of type fixation*. Kellogg's Mexican report (1932, *Bull. U. S. Nat. Mus.* No. 160) nicely covers part of this problem for his area but even he did not quite realize that mere assertion that a species is the type of a generic name is no guarantee of the correctness of the assertion. Generic type designations given by any author may not be correct at all. Only the additional citation of the *method* (by original designation, tautonymy, monotypy, or subsequent designation, and, if the latter, when, where and by whom first designated) clinches the matter. The importance of this minor but troublesome detail, in a fauna as nomenclaturally unstable as the Neotropical frog fauna, should be evident.

As Dr. Cochran says, her work is no complete and final analysis of the frogs of this rich tropical area, in which almost every collecting trip brings to light rarities or unrecognized forms. But her book will remain for a very long time as one of the principal and most useful anchorages in the poorly charted seas of South American batrachology.—GEORGE S. MYERS, *Natural History Museum, Stanford University, California.*

THE MARINE AND FRESH WATER

FISHES OF CEYLON. By Ian S. R. Munro. Department of External Affairs, Canberra: xvi + 351, 19 figs., 56 pls. Price not stated.—This treatise on the fishes of Ceylon was obviously patterned after J. L. B. Smith's widely acclaimed *Fishes of Southern Africa*, but differs in the lack of colored plates, in the less complete documentation, and in being more largely a compilation. As in Smith's book, the keys are artificial, much abbreviated, and, for many comparisons, limited to a single tersely stated character. The brief synonymies are restricted to the citation of the original description, a reference to the source of the copied figure, and a bare list, without authors, of other name combinations used in records for Ceylon. Again as in

Smith's book, the species descriptions are confined to rather terse diagnoses; these accounts are indicated as having been taken from the literature. The group names and the sequence are from Berg's 1940 Treatise. Most of the English vernaculars, which are complete for each species, were concocted, often with skill and appropriateness, from some characteristic of the fish, from the scientific name, or from some resemblance to a better-known though unrelated type. Sinhalese and Tamil names are compiled.

The species list is intended to be as complete as the published records warrant, and a great majority (714) of the 856 listed species are figured. The figures are photographic reproductions of somewhat diverse published illustrations. Crowded onto 56 half-tone plates, the figures lose some detail, though the photography and printing were excellent. This very crowding, however, facilitates comparisons, and presumably made the inclusion of so many illustrations feasible.

For the proffered purpose of this book, as a popular handbook for identification, the abundant illustrations will serve very well. The keys and descriptions will help too, especially since they are supplemented by neat and effective figures drawn by the author to portray differences in form and technical details in structure. Suggestions are given for the use of figures, diagnoses, and keys in the identification of specimens. A glossary is included.

In such a vast compilation it is no small wonder that an investigator noted for painstaking, penetrating, and precise research should have skidded a bit here and there. Some of the slips may be noted. A few species, including *Mugil cascasia*, seem to be listed in error for Ceylon. In the Cyprinodontidae the very diverse species *melastigma* and *panchax* are put in the same genus. Generic separation in the Sciaenidae seems antiquated. Blenniidae are wrongly keyed out from the Clinidae on the basis of the lack of a pelvic spine. *Remora scutata* is retained as a valid form, though long recognized as a synonym of *Remilegia australis*. The systematic treatment in general, however, is modernized and meticulous.

This well-printed treatise not only should prove very useful to fishery workers, students, and the interested public in Ceylon and India, but also should help, at least as a starting point, in the identification of fishes from other parts of the vast Indo-Pacific realm. It will be useful to students of zoogeography and the abundant illustrations will demonstrate to students in general the vast diversity of form among fishes. The author and his Australian governmental agency are to be congratulated on the parts they have respectively played in preparing and publishing this fine contribution for the people of a

country in which fishery science is less well developed.—CARL L. HUBBS, *Scripps Institution of Oceanography, University of California, La Jolla, California.*

SCIENTIFIC WRITING. By Meta R. Emburger and Marian R. Hall. Harcourt, Brace and Co., New York, 1955: xii + 468. \$4.50.—This book is an attempt to aid the scientist in the problems of communicating his findings to his colleagues. Chapters 1 to 6 deal with the intellectual activity preceding composition; chapters 7 to 9, the problems of communication; chapters 10 to 13, analyses of various types of papers; chapters 14 to 15, format, graphic and pictorial illustration. Technical writers will profit especially by reading chapter 8, "Scientific Style." Those concerned with popular writing will find much of value in chapter 7, "Directing the Paper to the Reader."

The herpetologist will read with pride and profit the analysis of a section, "The rattle", taken from *Field Book of Snakes* by Karl P. Schmidt and D. Dwight Davis. The extract is presented as an example of writing that maintains interest without sacrificing conciseness. Many other such analyses make this book of special value to the unskilled or inexperienced author interested in improving his writing.

The book not only emphasizes many significant generalizations pertinent to scientific writing, but provides specific, helpful suggestions to the writer. Its weakness lies in the authors' attempt to cover a large array of problems in various types of writing and their desire to make the book useful as both a text and a reference. The compromise is often awkward. This book is potentially of greater value as a text than as a reference. Other references of superior value to the scientific writer are available. However, there are no outstanding texts on scientific writing that place this degree of emphasis on the field of biology.—FRED R. CAGLE, *Department of Zoology, Tulane University, New Orleans, Louisiana.*

AN UNOFFICIAL INTERPRETATION OF THE INTERNATIONAL RULES OF ZOOLOGICAL NOMENCLATURE, AS AMENDED BY THE XIII INTERNATIONAL CONGRESS OF ZOOLOGY, PARIS, 1948 AND BY THE XIV INTERNATIONAL CONGRESS OF ZOOLOGY, COPENHAGEN, 1953. By W. I. Follett, September 1955, unpublished, v + 99 pages.

This splendid and concise account of the historic decisions relative to the International Rules of Zoological Nomenclature reached at the Paris and Copenhagen Congresses, prepared by the chairman of the Committees on Zoological Nomenclature of

the American Society of Ichthyologists and Herpetologists and the Society of Systematic Zoology, has just been distributed by the latter society. The report brings together for the first time and under one cover, a succinct, basic summary of the many important revisions and innovations made at the Paris sessions and subsequently modified at Copenhagen. These decisions have previously been available only in the expensive (\$32.00) fourth volume of the *Bulletin of Zoological Nomenclature* for the Paris Congress and in the more reasonably priced (\$1.75), but now out of print summary of the Copenhagen discussions in a special publication of the International Commission on Zoological Nomenclature. The former publication contains 760 pages the latter 135.

Dr. Follett has boiled down the excessive verbiage of the official documents and coordinated the decisions of the two separate congresses into a single orderly sequence. Changes initiated at Paris but revoked at Copenhagen are duly noted with the latest decision clearly stated in all cases. As presented, this paper gives an authoritative, up-to-date account of the present condition of The International Rules of Zoological Nomenclature, since the new rules as modified by the changes adopted at the two congresses are now in effect even though an official code has not yet appeared. Although an unofficial publication, Follett's summary is sure to be utilized as the basic nomenclatural guide for most American systematists until the revised International Code is published by the Commission.

The value of the publication is increased by cross-references to the official sources, which as Follett notes should always be consulted before final conclusions are reached. The report is further enhanced by an adequate index and is printed on good paper with margins wide enough for annotations. Although stated to be "unofficial" and "unpublished" on the title-leaf and in the introduction, it is doubtful that these statements will materially damage the overall usefulness or demand for this excellent work.

It is hoped that Dr. Follett and the Society of Systematic Zoology will make copies of the report available to non-members of that organization interested in the recent momentous changes in The Rules of Zoological Nomenclature.—JAY M.

SAVAGE, *Department of Zoology, Pomona College, Claremont, California.*

SALAMANDERS AND OTHER WONDERS. By Willy Ley. The Viking Press, New York, 1955: 1-293. \$3.95.—This book offers the reader a bit of the excitement and drama of biology while presenting honest knowledge. The herpetologist will admire the refreshing daring of Willy Ley in initiating readers with the title "Cave Salamanders and High Politics" and terminating his volume with an essay on turtles "The Old Ones." His blending of zoological knowledge with personalities, history, and mythology creates stimulating reading for both the zoologist and layman.

The familiar but effective writing procedure of leading the reader down the same trail followed by scientists in developing their knowledge is continued throughout each of the essays. This approach permits Ley not only to maintain interest but to present a surprising amount of information and to indirectly communicate appreciation of scientific methods. This technique weaves a thread of consistency throughout a book reporting on diverse botanical and zoological matters. Part I, "Problems of the Past" deals with cave salamanders, little people, nature as a teacher, abominable snowmen, and the origin of flight. Part II, "Botanical Interlude: Three Fabulous Trees" discusses the tales of the tree of death, the man-eating tree, and the emperor's *Arcanum Magnum*. Part III, "Survivors" tells of the cahow, the waldrapp, the sea otter, and the giant tortoises.

It is striking that Willy Ley, a free lance writer, managed to present more, substantial zoological knowledge than many zoologists have done in their popular writing. This provides support for the argument that the zoologist often underestimates his audience, a conclusion suggested by the records of other recent books written for the public. This book should be read by any zoologist interested in the presentation of zoological knowledge to the layman.

The book-jacket flattery does not exaggerate in claiming that the author's popularity and reputation as an interpreter of science for the layman have grown with every book. This is true. Ley has written a book that will be of interest to the layman and scientist alike.—FRED R. CAGLE, *Department of Zoology, Tulane University, New Orleans, Louisiana.*

EDITORIAL NOTES AND NEWS

Fifth Annual Meeting South-eastern Division

THE Fifth Annual Meeting of the Southeastern Division, ASIH, was held on October 7-8, 1955, at the Highlands Biological Station, North Carolina. The meeting was arranged by THELMA HOWELL, director of the Station. Thirty-seven people were in attendance, representing fourteen institutions and organizations in the Southeast. The following papers were presented on the morning of October 7:

Frogs of the *Rana areolata* Group in the Southeastern States.—Wilfred T. Neill, Research Div., Ross Allen Reptile Institute, and William E. Brode, Copiah-Lincoln Junior College, Wesson, Miss.

A Non-adaptive Aspect to the Coral Snake 'Mimic' Problem.—Arnold B. Grobman, Florida State Museum.

Notes on a Population of *Chologaster papillifera*.—William M. Clay and William Weber, Univ. of Louisville.

Delayed Appearance of a Coronoid Bone in Certain Bolds.—T. P. Haines, Mercer Univ.

Further Contributions to our Knowledge of the Striped Musk Turtle, *Sternotherus carinatus peltifer* Smith and Glass.—Richard M. Johnson, Tennessee Wesleyan College.

Time, Place, and the Permanent Record.—William J. Riemer, Florida State Museum.

Reports of Progress in Research at the University of Florida, Florida State Museum, Florida State University, Duke University, Ross Allen Reptile Institute, Wesleyan College, University of Louisville, Mercer University, Tulane University, Davidson College, Mississippi Southern College, Tennessee Wesleyan College, and the Highlands Biological Station.

The following officers were elected by unanimous ballot, to serve during 1956: *President:* WILFRED T. NEILL (Research Division, Ross Allen Reptile Institute) *Vice-President:* JOSEPH R. BAILEY (Department of Zoology, Duke University) *Secretary-Treasurer:* ELMER E. BROWN (Davidson College)

On the afternoon of October 7, the group visited Whiteside Mountain and the Margaret Cannon Howell Wildlife Refuge. That night, following the annual dinner, there was an informal discussion, *Ecology of the Highlands, North Carolina, Area*, led by EUGENE P. ODUM, Univ. of Georgia.

The Highlands region being of exceptional biological interest, October 8 was devoted largely to field trips.

New Institute of Fisheries

A New Institute of Fisheries has been organized recently at the University of British Columbia. It is intended to provide graduate students with broad instruction in the field of fisheries, including training in basic biology and in

the more practical aspects of the use and management of fisheries resources. It is also designed for those students who are seeking the Master's or Doctor's degree. The institute is directed by a Committee on Fisheries representing the cooperating divisions within the University.

The staff includes Dr. P. A. LARKIN (Director), Dr. W. A. CLEMENS, Dr. C. C. LINDSEY, Dr. W. S. HOAR, and Mr. M. A. NEWMAN. Mr. NEWMAN is Curator of the rapidly expanding research Museum, which now contains more than 5,000 specimens. The museum is currently active in making exchanges and requests exchanges of scientific specimens from similar institutions. Requests for details regarding the Institute, including scholarships, should be addressed to the Director.

University of Maryland

THE Zoology Department of Maryland, has recently enlarged its program in fisheries. Members of the staff now include: Dr. LITTLEFORD, who is in charge of the new Seafood Processing Laboratory of the Zoology Department at Crisfield on the eastern shore of Chesapeake Bay; Dr. ALLEN, invertebrate zoologist, working on shellfish and fish management; and three new members, Dr. BENARDE, food technologist and bacteriologist; Dr. LIVINGSTONE, ecologist and limnologist; and Dr. WINN, behaviorist and ichthyologist.

A full program of undergraduate and graduate studies is available for students on both pure and applied aspects of the taxonomy, biology and technology of freshwater and marine fishes. Graduate students can obtain teaching assistantships or other part time positions. The Patuxent Research Refuge (U. S. Fish and Wildlife Service); Chesapeake Biological Laboratory, Solomons, Maryland; U. S. National Museum; Chesapeake Bay; and numerous streams and impoundments are all within easy reach and are potential areas where studies can be carried out. An aquarium room has been established in the Zoology Building.

University of Florida

PRESENT and recent doctoral students at the University of Florida include:

Dr. JOHN CRENSHAW, who completed his program during the summer of 1955, is now Assistant Professor of Zoology at the University of Missouri. His thesis, "The relationship and distribution of the

Pseudemys scripta complex," was under the direction of Dr. ARCHIE CARR.

Dr. KEITH HANSEN, now Assistant Professor of Biology at Stetson University, also finished his program during the summer of 1955. Dr. COLEMAN J. GOIN directed his thesis, "A study of *in vitro* ovulation in the spadefoot toad, *Scaphiopus holbrooki*."

Dr. WILLIAM M. McLANE, who is with the Florida State Game and Fresh Water Fish Commission, recently completed the work for his degree. His thesis, "Fishes of the St. Johns," was done under the direction of Dr. GOIN.

WALTER A. AUFFENBERG, whose thesis research is "The fossil snakes of Florida," plans to complete the studies for his degree in the summer of 1956. Dr. ARNOLD B. GROBMAN is chairman of his Supervisory Committee.

RICHARD HIGHTON's thesis research, under the direction of Dr. GROBMAN, is "The relationships of the salamanders of the genus *Plethodon*." Mr. HIGHTON spent the summer of 1955 as a ranger-naturalist in the Great Smoky Mountains National Park, where he was able to assemble fresh material for his study. He plans to complete his degree program by next summer.

DAVID CALDWELL is working on the biology of the pin fish, *Lagodon rhomboides*, with Dr. CARR. He spent part of the summer marking green turtles as part of Dr. CARR's migration study.

RICHARD JOHNSON, who is Assistant Professor of Zoology at Tennessee Wesleyan College, is continuing his studies under Dr. CARR's direction. His thesis problem is "Amphibians and reptiles of east Tennessee."

Florida State Museum

WILLIAM J. REIMER, who received his training with Dr. ROBERT C. STEBBINS at the Museum of Vertebrate Zoology, Berkeley, has joined the staff of the Florida State Museum as Assistant Curator of Biological Sciences. His major responsibility is the collection of amphibians and reptiles cooperatively maintained by the Museum and the University of Florida's Department of Biology. Mr. REIMER is also teaching the herpetology course. Three members of the Department are Associates of the Museum and share in the development of the collections: in herpetology, Dr. ARCHIE CARR; in ichthyology, Dr. JOHN D. KILBY and Dr. JOHN C. BRIGGS.

As part of a biological survey of the Flint-Chattoahoochee-Apalachicola River Drainage basins in West Florida, the staff and Associates are studying the fishes, amphibians and reptiles of the area. The investigation is being sponsored by the National Park Service and the National Science Foundation.

The Saylor Awards in Fisheries University of Michigan

THESE awards were established in 1955 by an annual contribution to the Trust Fund for Fishery Research in the University by outdoorsman-conservationist FRANK D. SAYLOR, JR. Two are given each year to students in the Department of Fisheries, School of Natural Resources, who show particular competence and promise. Each award is a five-year membership in the American Fisheries Society. Recipients are selected by the staff of the department.

ASIH 1956 Annual Meeting

THE 36th annual meeting of the Society will be held at the Conservation Training School, Higgins Lake (near Roscommon), Michigan, on June 21-24. The Board of Governors will meet at the Training School at 8 P.M. on June 20. A call for papers will be mailed to the membership during March. At that time information on housing accommodations at the Training School, motels, and camping facilities will be provided. Titles of papers, addressed to the Program Chairman, Charles F. Walker, Museum of Zoology, University of Michigan, Ann Arbor, Michigan, must be received prior to May 1 to be included in the program. The American Society of Mammalogists will utilize the same facilities for their annual meeting which will be held June 16-20. Members of the local committee include: Reeve M. Bailey (local chairman), Gerald P. Cooper, Paul H. Eschmeyer, Norman E. Hartweg, Karl F. Lagler, Robert R. Miller, Stanford H. Smith, and Charles F. Walker.

Copela Malling Dates, 1955

COPIES of COPEIA for 1955, mailed first-class to the Editor-in-Chief, were postmarked at Baltimore, Maryland as follows: No. 1 on February 19, No. 2 on May 21, No. 3 on August 23, and No. 4 on November 21.—G.P.C.

News Notes

SPORT Fishery Abstracts, a serial to be issued irregularly by the Branch of Federal Aid of the U. S. Fish and Wildlife Service, was initiated in July, 1955. Its purpose is "to furnish fishery biologists in government agencies and educational institutions with abstracts of the current literature in sport fishery research and management." Nearly 200 North American publications and 7 British journals are to be abstracted in the first volume. *Sport Fishery Abstracts* may be obtained free by qualified individuals.

On December 1, 1955, Dr. ALBERT S. HAZZARD resigned as Director of the Michigan Conservation Department's Institute for Fisheries Research, at Ann Arbor, to accept appointment as Assistant

Executive Director of the Pennsylvania Fish Commission, of which the well-known conservationist WILLIAM VOIGT is Executive Director. Dr. HAZZARD was the first full-time Director of the Institute for Fisheries Research, a position he filled for 20 years. Dr. GERALD P. COOPER, former Editor-in-Chief of this journal, replaces Dr. HAZZARD in the Michigan position.

Dr. RAYMOND C. OSBURN, emeritus head of the zoology department at Ohio State University, who early worked on the fishes of Ohio and who collaborated in the biological survey of the Woods Hole region, died on August 8, 1955.

Dr. GORDON GUNTER has resigned as Director of the Institute of Marine Science of the University of

Texas to accept an appointment as Director of the Gulf Coast Research Laboratory at Ocean Springs, Mississippi. This laboratory is operated by the Board of Trustees of the Institutions of Higher Learning of the State of Mississippi. The laboratory is thus affiliated with all the state colleges of Mississippi but is separately administered.

Microcards of four volumes of reprints (140 reprints; about 4,100 pages) on herpetology collected by the U. S. National Museum, 1823-1876, are available from FRED R. CAGLE, Meade Natural History Library, Tulane University, New Orleans, La. These will be sold for the cost of manufacture and distribution, \$20.00 per set. Sets cannot be broken. Lists of reprint titles will be sent on request

A.S.I.H. BOARD OF GOVERNORS, 1956

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